PALEOECOLOGY OF TWIN CAYS: INTERPRETATION OF PALYNOLOGICAL, ISOTOPIC, AND STOMATAL PROXIES IN A PEAT CORE FROM BELIZE

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Abstract

Reconstructions of Holocene climate from numerous mid- and high-latitude sites have identified millennial-scale cool and arid intervals at ~8,200 and ~4,200 yrs. B.P. The global nature of these events can only be established by examination of Holocene climate records from low latitude sites. The Central American island of West Twin Cays was chosen as the study location due to its thick peat deposits, which allow for the reconstruction of Holocene vegetation, sea level, and climate for the Belize coastal region. *Rhizophora mangle* (red mangrove) dominated the island's vegetation since its formation ~8,200 cal. yrs. B.P. Alternating periods dominated by dwarf or tall *R. mangle* reflect changes in phosphorus and nitrogen availability. Heightened *Myrsine*-type pollen concentrations between ~6,300 and ~4,200 cal. yrs. B.P. suggests lower sea levels and drier climates. Regional warming accompanied by increased precipitation in the middle to late Holocene is recorded by an increase in exotic *Pinus* concentrations. These vegetation shifts correlate with regional Central American climate changes and western Atlantic sea level shifts at ~8,200 and ~4,200 cal. yrs. B.P. More importantly, these data link Central American changes to worldwide climate events.

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Chapter 1: Introduction

1.1: Rational

Holocene climate change and sea level transgressions have dramatically impacted coastal areas, including many low elevation islands off the coast of Belize (Macintyre et al., 1995). A variety of mangrove species have been present in Belize since the early Holocene. These maritime trees inhabit saline areas and are often found inundated with seawater. Because mangroves are sensitive to sea level changes (Woodroffe, 1995; Murray et al., 2003; Wooller et al., 2004), they can be useful for reconstructing paleoenvironments.

The chosen study location is Twin Cays, a pair of low elevation islands located off the central coast of Belize (Fig. 1.1). The islands have been dominated by mangrove vegetation since their formation approximately 8,200 calendar years before present (cal. yrs. B.P.) (Wooller et al., 2004). The mangrove species present on Twin Cays include *Rhizophora mangle L.* (red mangrove), *Avicennia germinans* [L.] Stearn. (black mangrove), and *Laguncularia racemosa* [L.] Gaertn. f. (white mangrove) (Koltes et al., 1998; McKee et al., 2002; Wooller et al., 2004).

Sea level change is the primary influence on mangrove development and zonation (McKee and Faulkner, 2000; Wooller et al., 2004). Three mangrove species are present on Twin Cays, and each

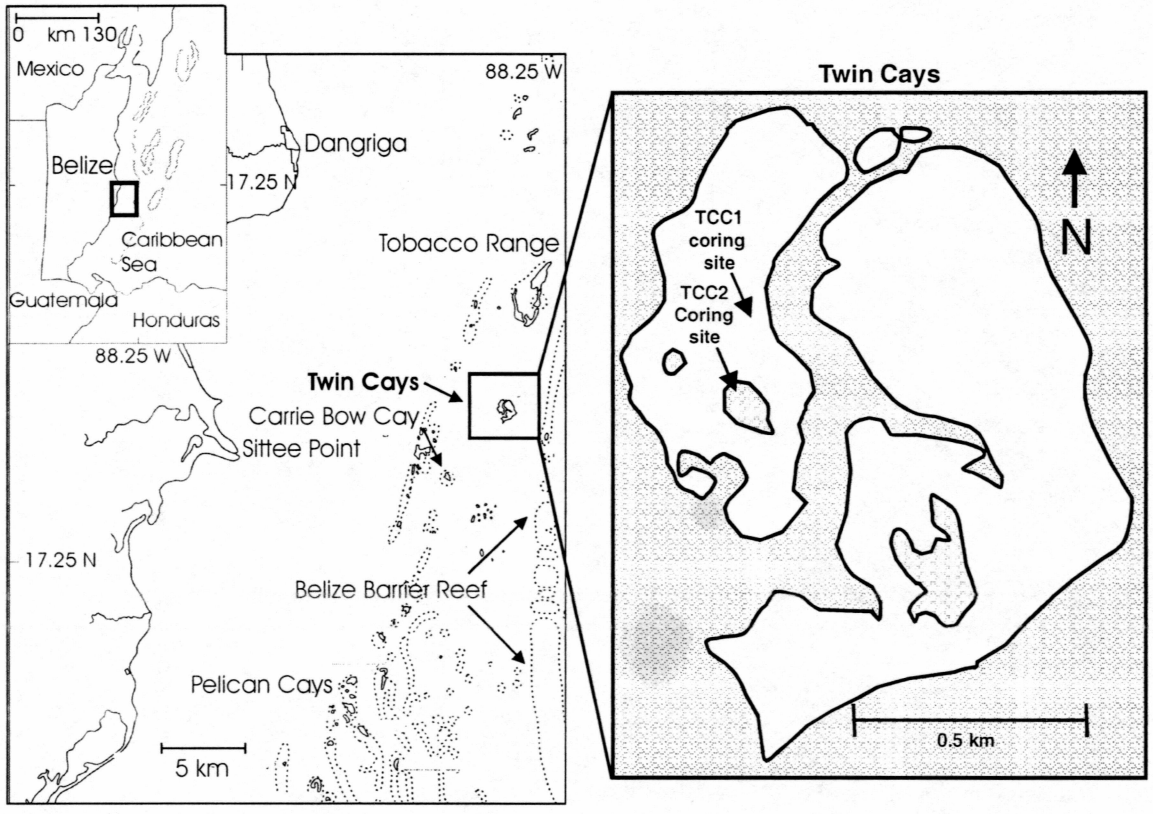

Figure 1.1
Twin Cays study location and core sites.
Map showing islands off the coast of central Belize, including Twin Cays and surrounding islands (modified from Wooller et al., 2004).

inhabits a separate niche (Wooller et al., 2004). *R. mangle* (red mangrove) is common along the coast or inland pond areas, frequently inundated with seawater. *A. germinans* (black mangrove) occupies interior regions with higher relative salt concentrations, and *L. racemosa* (white mangrove) occupies inland regions with slightly higher elevations and lower salt concentrations (Fig. 1.2) (McKee and Faulkner, 2000, Wooller et al., 2004). Twin Cays is composed of lowland areas, so *L. racemosa* is sparse. Where present, it is intermixed with *R. mangle* and *A. germinans* forests. Because these three species have different ecological tolerances and requirements (i.e. salinity), minor sea level changes can dramatically affect their distribution.

Sea level changes, nutrient shifts, and storm damage can drastically alter subtropical mangrove habitats (Kuenzler, 1974; Woodroffe, 1995; Ellison and Farnsworth, 1996; Murray et al., 2003; Wooller et al., 2004). In 1992, Hurricane Andrew passed over Florida, killing 35-38% of the mangroves (Baldwin et al., 2001). As a result, the forest structure was significantly altered; a forest previously dominated by *R. mangle* became highly mixed with herbaceous species after the storm (Fig. 1.3) (Baldwin et al., 2001).

Previous paleoecological studies have shown that the most effective approach to interpreting environmental change is to integrate data from multiple proxies (Wooller et al., 2003; Wooller et al., 2004).

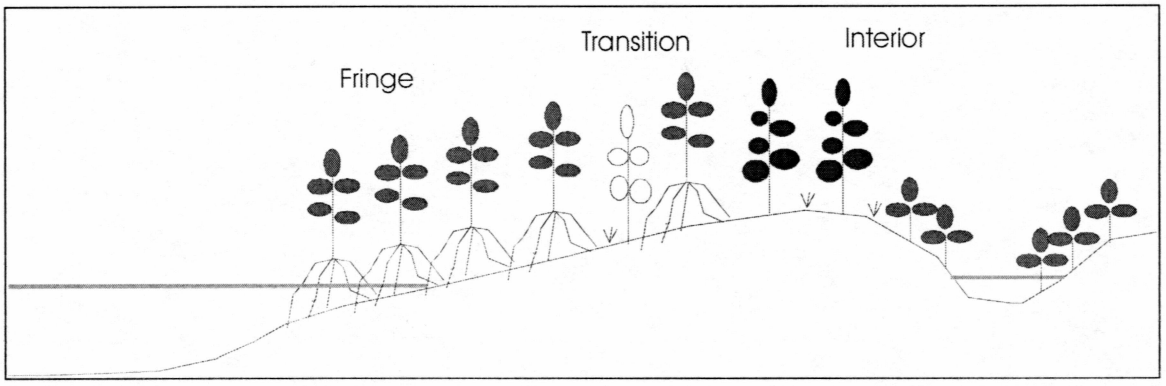

Figure 1.2
Mangrove zonation on Twin Cays.
The fringe area is dominated by tall *Rhizophora mangle* represented by the tall gray trees. The transition zone is primarily *R. mangle* with scattered *Laguncularia racemosa* (white trees). Interior areas are typically characterized by *Avicennia germinans* (black trees), while interior ponds are surrounded by dwarf *R. mangle* stands (short gray trees) (modified from McKee and Faulkner, 2000).

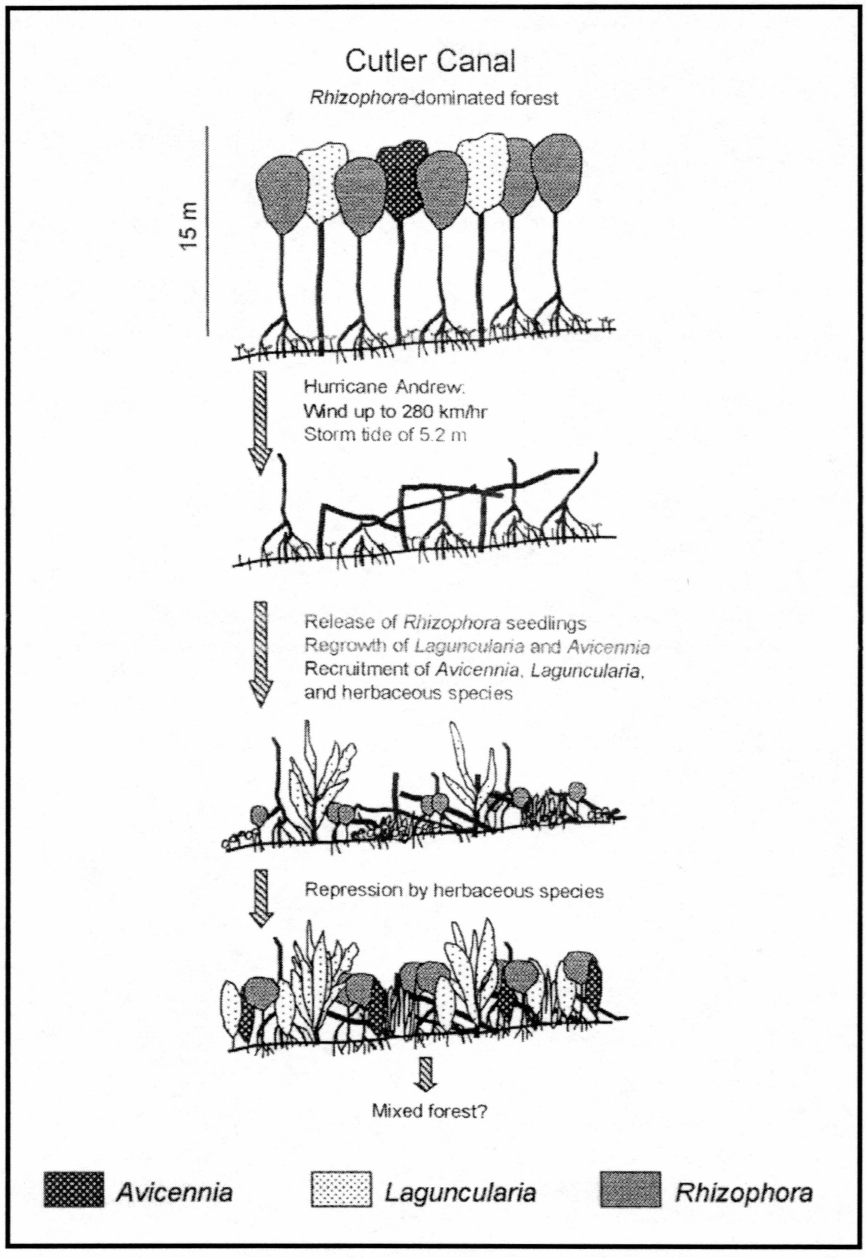

Figure 1.3
Mangrove succession following destruction caused by a hurricane. This diagram shows the forest structure before and after hurricane Andrew passed through Florida. High winds and tidal surges devastated many of the coastal *R. mangle* forests, which subsequently, were replaced by mixed forests containing mangroves and herbaceous species (modified from Baldwin et al., 2001).

Palynology and stable isotope analyses (carbon and nitrogen in particular) are valuable for reconstructing paleoenvironments (Wooller et al., 2004). This paper integrates palynology and stable isotope methods with preliminary stomatal analyses. These methods are useful for determining vegetation distribution and nutrient shifts.

A number of ecology studies have been conducted on Twin Cays, Belize (Feller et al., 2003; Smallwood et al., 2003; Wooller et al., 2003; Wooller et al., 2004). Previous research indicates widespread vegetation and sea level shifts occurred throughout the Holocene especially at ~8,200 and ~4,200 cal. yrs. B.P. (see Wooller et al., 2004). These periods are recorded as arid intervals in the northern hemisphere but little research has been done in the southern hemisphere or the Central American region. *R. mangle* dominates the Twin Cays vegetation throughout the Holocene except at 4,260 cal. yrs. B.P., when it decreased in abundance (Wooller et al., 2004). Following this decline, a ~200 year interval is dominated by *Myrsine*-type vegetation (Wooller et al., 2004). This major vegetation shift is interpreted as the result of either a hurricane or a drop in sea level (Wooller et al., 2004). My main objective is to determine whether this was a local or regional change and to reconstruct other Holocene paleoecological shifts recorded on Twin Cays.

1.2: Background

1.2.1: Mangrove Habitat

Mangroves are temperature sensitive and survive only in areas with average water temperatures warmer than 23°C (73°F) (Rützler and Feller, 1996). Thus, they are restricted to a belt between 25°N and 25°S latitude (Kuenzler, 1974). Mangroves are distributed worldwide in this equatorial zone. They are found primarily in Africa, Australia, northern South America, eastern Asia, and the Middle East (Woodroffe and Grindrod, 1991) due to the warm climates and low elevation coastlines.

R. mangle exhibits variation in growth forms (Wooller et al., 2003; Wooller et al., 2004). A variety of growth forms ranging from a dwarf (<1.5 m) to tall (1.5 to 10 m) are found on Twin Cays (Feller, 1995; Woodroffe, 1995; Koltes et al., 1998; McKee et al., 2002). The growth of the dwarf form is limited by phosphorus availability and occupies areas with abundant nitrogen; tall *R. mangle* growth is limited by nitrogen availability but never uses all the available phosphorus (Cameron and Palmer, 1995; Feller, 1995; Woodroffe, 1995; Koltes et al., 1998; McKee et al., 2002). A transitional growth form, co-limited by both nitrogen and phosphorus, includes trees ~2-4 m tall (McKee et al., 2002). Variation in *R. mangle* height caused by nutrient deficiency is apparent on many coastal islands in the Belize barrier reef (Woodroffe, 1995).

Dwarf and tall *R. mangle* trees cannot be distinguished using palynological analyses, but they have different stable carbon and nitrogen isotope signatures (Wooller et al., 2003; Wooller et al., 2004). Leaves from tall *R. mangle* trees generally exhibit stable carbon isotope values ($\delta^{13}C$) of ≤-27‰ and stable nitrogen isotope values ($\delta^{15}N$) from -2.8 to +3.2‰ (Wooller et al., 2003; Wooller et al., 2004). The dwarf trees are characterized by $\delta^{15}N$ values ≤-3‰ with $\delta^{13}C$ values between -24 and -26‰ (Wooller et al., 2003).

1.2.2: Introduction to Mangrove Ecology and Biogeography

Many factors can contribute to the dieback of mangrove forests, including salinity, hurricanes, sea level changes, or nutrient fluctuations. Shoreline erosion and, consequently, mangrove distribution on Twin Cays may be influenced by environmental stresses resulting from hurricane damage, reduced tidal flushing because of sea level regression, salinity, or deforestation (Woodroffe, 1995).

Heightened salinity concentrations have been proven to cause mangrove dieback in some regions (e.g. Puerto Rico); many mangroves perish when salinity concentrations are greater than 65 parts per thousand (ppt) (Cintrón et al., 1978; Woodroffe, 1995). These heightened salt concentrations are often a result of reduced tidal flushing and evaporation, which can create hypersaline interior ponds. Salinity

measurements taken from the unvegetated flats of Twin Cays are similar to values collected in open water areas (38 ppt) (Woodroffe, 1995). The highest salinity levels recorded on Twin Cays (58 ppt) occur under healthy *A. germinans* plants (Woodroffe, 1995). Current salinity measurements are consistently lower than those causing mangrove mortality, but salinity levels may have been much different in the past.

Tropical storms and hurricanes have a great influence on mangrove development. These storms are relatively frequent in Belize. Since 1951, seven major hurricanes have hit the country, and many more have passed nearby (Table 1.1) (Belize Hurricane Net, 2003). In addition to the vegetation destruction that accompanies these storms, there is often increased erosion (Baldwin et al., 2001). Hurricanes can change topography through the actions of floodwaters, which rework and deposit sediments (Murray et al., 2003). Many of the islands in the Belizean barrier reef are constructed of mangrove peat, which is highly susceptible to erosion (Macintyre et al., 1995; Woodroffe 1995). These atolls, surrounded by water and nearly at sea level, have little protection from storm waves.

Hurricane Hattie passed just north of Twin Cays in 1961 (Belize Hurricane Net, 2003). Today the effects of this storm are still present.

Table 1.1
Hurricane statistics for Belize over the past 50 years.
H means the hurricane directly hit the country of Belize. T stands for a light touch. A light touch indicates that the storm passed nearby and the island experienced some damage (modified from Belize Hurricane Net, 2003).

Year	Hurricane
1945	2 un-named
1950-1953	none
1954	Gilda (T)
1955-1959	none
1960	Abby (T)
1961	Anna (H), Hattie (H)
1962-1968	none
1969	Francelia (H)
1970	none
1971	Chloe (T), Edith (H), Laura (T)
1972-1973	none
1974	Fifi (H), Carmen (H)
1975-1976	none
1977	Freida (T)
1978	Greta (H)
1979	none
1980	Hermine (T)
1981-1992	none
1993	Gert (T)
1994-1999	none
2000	Keith (H)
2001	Iris (H), Chantal (T)

Mangrove stumps are found on Belize barrier reef islands (Woodroffe, 1995). It is assumed that these stumps represent trees damaged by the 1961 hurricane, since it was one of the most destructive storms in the past 50 years (Woodroffe, 1995). There is no evidence of mangrove destruction at Twin Cays, but it is believed that the 1961 hurricane destroyed the island's vegetation and altered the shoreline by erosion. *Avicennia* stumps on nearby Tobacco Range (Fig. 1.1) document the storm damage. *R. mangle* on Twin Cays may have also been devastated as a result of this hurricane, but wood preservation is poor for this species (Woodroffe, 1995). Since *R. mangle* stumps are the first to rot away, there is no remaining evidence of this destruction. Dwarf *R. mangle* have since colonized the disturbed areas.

In 1992, mangrove forest disturbance was documented across the state of Florida by *R. mangle* stumps left in the wake of hurricane Andrew (Fig. 1.3) (Baldwin et al., 2001). Similar damage was recorded along the Belize barrier reef. Severe storms have occurred repeatedly in the Caribbean and Central American regions so, it is likely that the vegetation of Twin Cays has been damaged or destroyed by storms on a regular basis.

1.2.3: Regional History and Geology

Belize is located on the Yucatan continental block (Fig. 1.4). This landmass rotated from its location near the equator along the West coast of Pangea to its present position during the early Triassic (Garcia and Holtermann, 1998), creating the Gulf of Mexico (Pindell et al., 2000). During the Pliocene, the entire block tilted northward due to extension and faulting (Cameron and Palmer, 1995; Garcia and Holtermann, 1998). Evidence for this northward tilting is provided by Pliocene normal faults trending north-northwest (Cameron and Palmer, 1995). Fault scarps were created, as evidenced by five parallel submarine ridges along the eastern edge of the modern Yucatan block (Fig. 1.5) (Burke, 1993; Cameron and Palmer, 1995; Garcia and Holtermann, 1998). Pliocene faulting and tilting created elevated blocks of land. Shallow water environments encouraged coral formation throughout the Pleistocene (Cameron and Palmer, 1995). During the last glacial maximum, when sea levels were low, some areas of the reef emerged above sea level and began to erode (Woodroffe, 1995). Approximately 9,000 years ago, the continental shelf around Belize flooded, and the elevated Pleistocene platforms were submerged (Macintyre et al., 1995). Shallow areas atop the Pleistocene reef created an ideal environment for mangrove development and island formation.

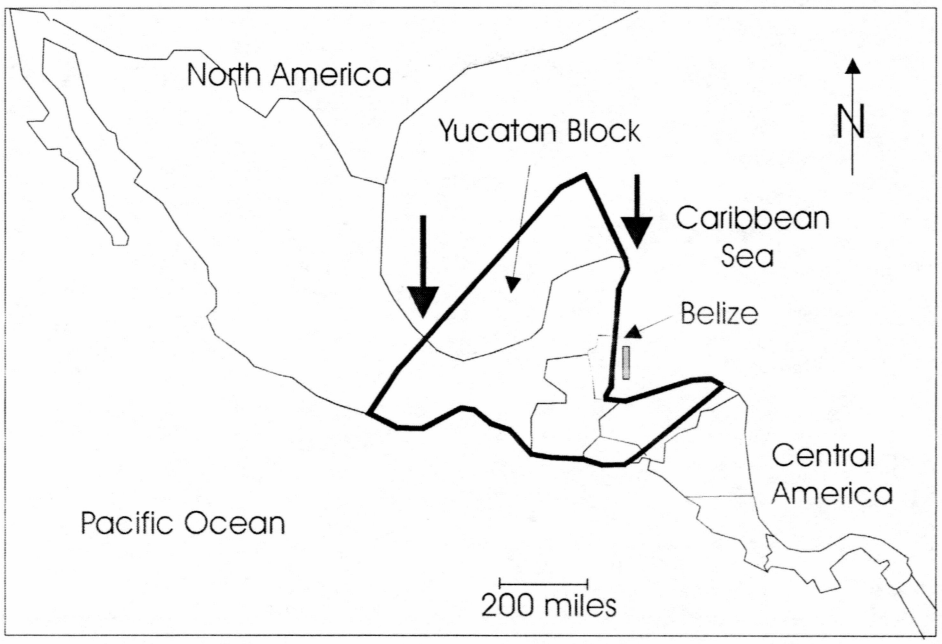

Figure 1.4
Central America showing the location of the Yucatan Block.
Bold arrows indicate the direction of movement from the Pangea landmass. The gray rectangle off the coast of Belize shows the area occupied by fault scarps (see Fig. 1.5) (modified from Kozuch, 1997).

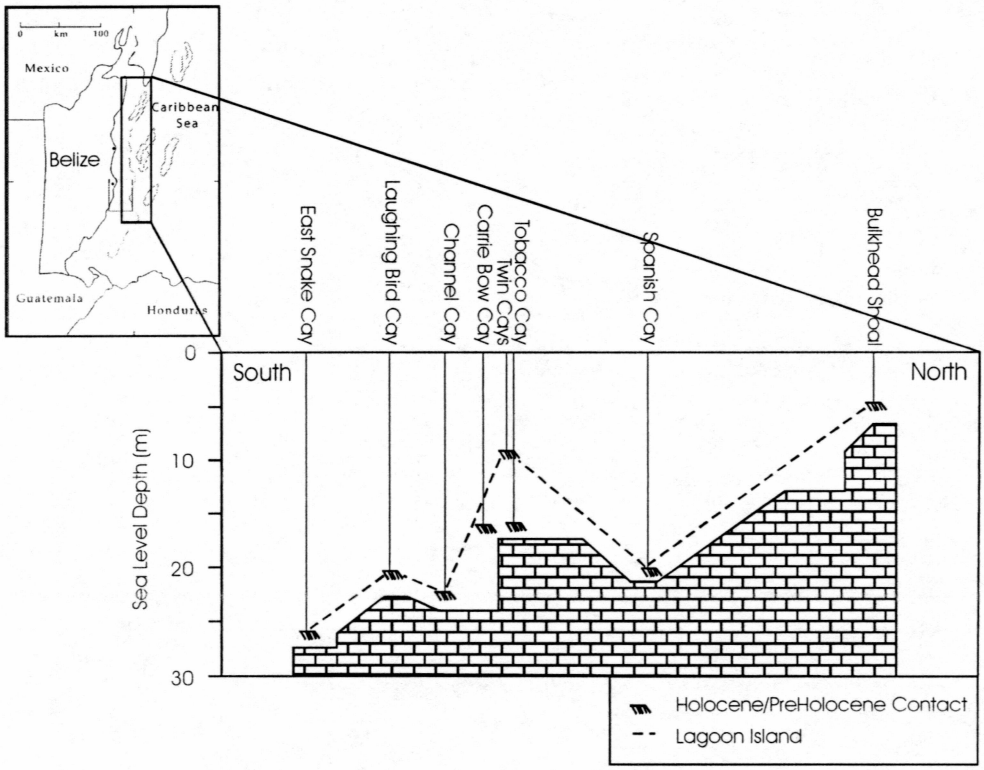

Figure 1.5
Belize coastal rifts.
This diagram is a cross section of the current Belize barrier reef. The brick pattern is the Pleistocene limestone reef underlying the Belize coastal islands. Mangrove peat lies between the Pleistocene limestone and modern land surface at 0 m depth (modified from Burke, 1993).

Mangroves only become established in low energy areas protected from wave erosion (Cameron and Palmer, 1995). Throughout the Belize barrier reef, mangroves began to develop shortly after Holocene sea level began to rise (between 9,000 and 8,000 cal. yrs. B.P.) (Macintyre et al., 1995). Around 8,200 cal. yrs. B.P., mangroves appeared on Twin Cays (Toscano and Macintyre, 2003; Wooller et al., 2004). Between ~8,200 and ~8,000 cal. yrs. B.P., sea level rose rapidly (up to 4.3 m/1,000 yrs.) (Littler et al., 1995; Macintyre et al., 1995). Many islands could not keep pace with the dramatic sea level increase and were swamped (Cameron and Palmer, 1995; Macintyre et al., 1995). Others, in the southern region of the Belize barrier reef returned to active reef formation (Macintyre et al., 1995). The remaining islands, like Twin Cays, were covered by mangrove vegetation.

1.2.4: Climate and Climate Change

Shortly after the last glacial maximum, global climate began to shift. Northern hemisphere climate change has been well documented for the late Pleistocene and early Holocene (Severinghaus and Brook, 1999; Dean et al., 2002; Shuman et al., 2002; Kurek et al., 2004). By comparison, variations in southern hemisphere and equatorial climates are broadly constrained for this period.

In the late Pleistocene (~13,000 cal. yrs. B.P.) Central America was cool and dry, with temperatures approximately 4 to 5°C cooler than today (Bush and Colinvaux, 1990; Markgraf, 1993). The interval from 13,000 to 10,000 cal. yrs. B.P. lacks arboreal pollen in lacustrine sediment cores (Markgraf, 1993; Leyden, 2002), indicating the existence of savanna-type vegetation (Markgraf, 1993). At ~9,000 cal. yrs. B.P., moisture levels were equal to or higher than today, but temperatures were still cooler than present. After 8,500 cal. yrs. B.P. precipitation decreased, reaching maximum aridity around 6,000 cal. yrs. B.P. (Markgraf, 1993).

At ~8,000 cal. yrs. B.P. the Central American climate cooled (Markgraf, 1993). This temperature decrease is not a local event; similar trends are seen throughout the northern hemisphere. Approximately 8,470 cal. yrs. B.P., the Laurentide Ice Sheet began to break apart. As the Hudson Bay ice mass melted, a pulse of freshwater entered the northern Atlantic Ocean (Shuman et al., 2002; Kurek et al., 2004). This altered ocean circulation and caused regional cooling. Climatic shifts attributed to this circulation change are seen in North America (Dean et al., 2002) and Europe (Shuman et al., 2002). A temperature decrease of 6±2°C occurred over Greenland between 8,400 and 8,000 cal. yrs. B.P. (Kurek et al., 2004). Although not well documented, Caribbean and Central American regions were affected by the alteration of ocean

currents and possibly experienced a decrease in sea surface temperatures (Lachniet et al., 2004).

From 5,000 cal. yrs. B.P. to present, the climate across Central America was variable, making it difficult to correlate regional climatic records (Markgraf, 1993). Agricultural disturbance in Central America began ~3,500 cal. yrs. B.P. (Pohl et al., 1996), and widespread land use impact after 2,500 cal. yrs. B.P. may have contributed to the variability (Markgraf, 1993; Islebe et al., 1996). Overall, regional temperatures have gradually increased during the Holocene.

Belize currently has a sub-tropical climate with a mean summer temperature of 36.6°C and a mean winter temperature of 22.5°C (Koltes et al., 1998). The wet season is from June to October, with an average rainfall of 1,000 mm per year on Twin Cays (Woodroffe, 1995). Precipitation on the coastal islands of Belize is significantly less than on the central and southern mainland. For instance, more than 2,000 mm of rainfall is measured annually at Dangriga, only ~12 km West of Twin Cays (Fig. 1.6) (Littler et al., 1995; Woodroffe, 1995). Northeast trade winds are present in this region approximately 70% of the year (Littler et al., 1995; Koltes et al., 1998).

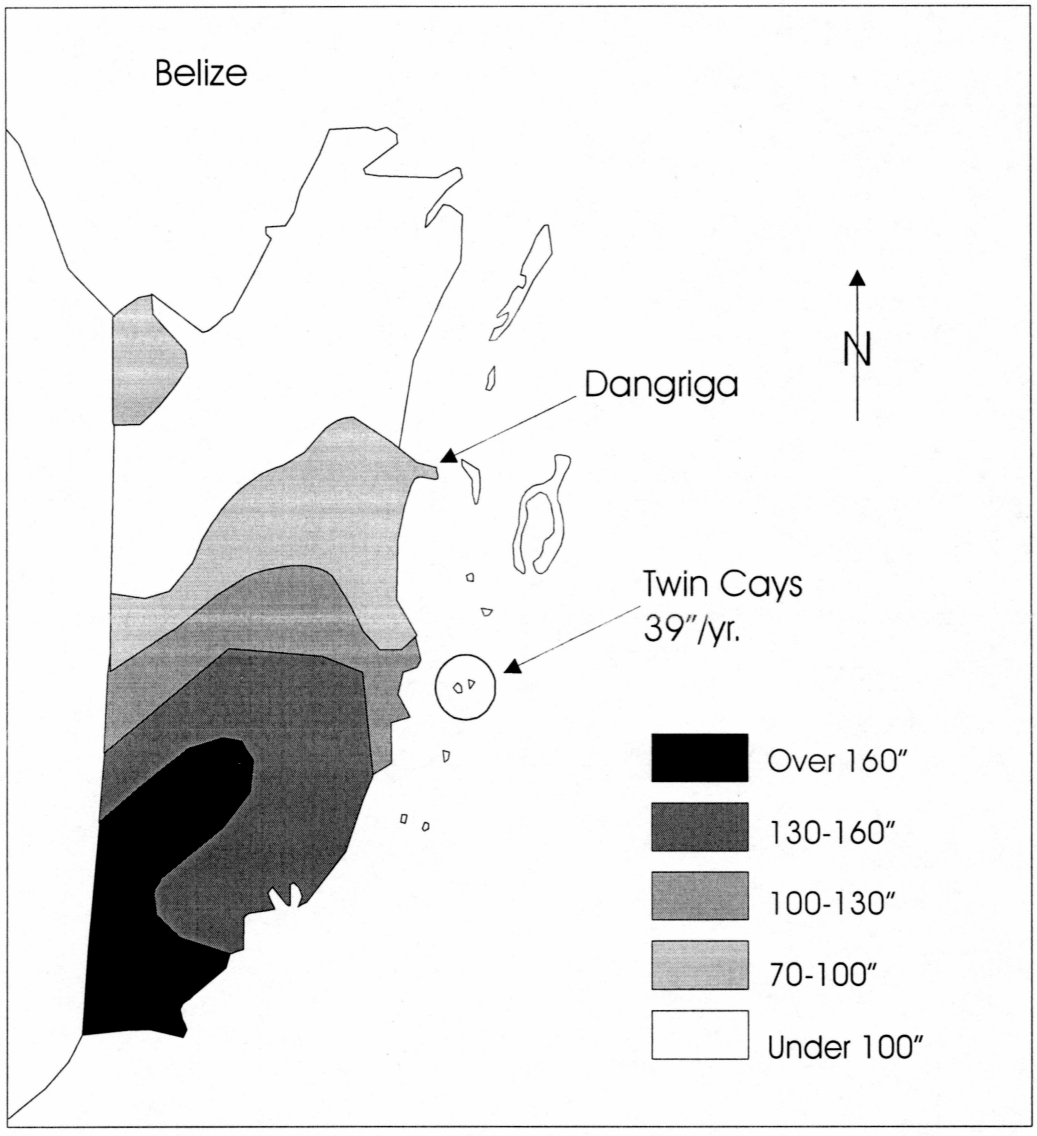

Figure 1.6
Current rainfall patterns for Belize and the coastal islands.
The coastal islands receive significantly less precipitation than the southern mainland. Twin Cays (circled) average 39" of rain per year (modified from Belize by Naturalight, 2005).

1.2.5: Holocene Atmospheric Carbon Dioxide Concentrations

Atmospheric carbon dioxide levels can influence climate through the insulating effect of this greenhouse gas. Studies of stomata and ice cores have shown that atmospheric CO_2 fluctuated throughout the late Pleistocene and Holocene (Oeschger et al., 1984; Hogan et al., 1991; Raynaud et al., 2000). Between 13,000 and 9,000 cal. yrs. B.P., an atmospheric CO_2 decrease of 70 ppm is documented by the examination of ice cores (Oeschger et al., 1984). By 9,000 cal. yrs. B.P., stomata and ice cores studies indicate carbon dioxide concentrations were near pre-industrial levels of ~290 ppm (Hogan et al., 1991; Raynaud et al., 2000; Royer, 2001). Around 200 cal. yrs. B.P. a rapid increase in CO_2 began. With the onset of the industrial revolution and burning of fossil fuels, larger amounts of carbon dioxide were released into the atmosphere. Presently, atmospheric CO_2 levels are near 370 ppm (Hogan et al., 1991; Raynauld et al., 2000; Royer, 2001) and continue to increase (Hogan et al., 1991; Royer, 2001).

1.2.6: Holocene Caribbean and Western Atlantic Sea Level Shifts

Sea level changes directly affect mangroves, especially in low-lying areas such as the Belize coastal islands (Macintyre et al., 1995; Wooller et al., 2003). Since mangroves inhabit lowland, marshy areas, slight increases in sea level can flood plants. Marine regressions cause excess

erosion and destroy peat buildup underlying the mangrove forests, reducing area. Thus, peat is a useful indicator of sea level advances, but nearly useless for recording sea level retreat (Kearney, 2001).

Global sea level has risen throughout the Holocene (Lighty et al., 1982; Toscano and Macintyre, 2003). During the last glacial maximum, sea level was ~125 m lower than present (Fairbanks, 1989; Bard et al., 1990). As gradual warming occurred, sea level began to rise. Toscano and Macintyre (2003) have compiled sea level data for many Caribbean regions including Florida, Belize, Jamaica, and Panama (Fig. 1.7). This research suggests that the Holocene sea level transgression (from 10,000 through 3,000 cal. yrs. B.P.) was more rapid than previously thought.

Peat-forming mangroves were established on Pleistocene limestone off the coast of Belize between 8,000 and 7,000 cal. yrs. B.P. (Cameron and Palmer, 1995; Littler et al., 1995; Woodroffe, 1995; Koltes et al., 1998). At this time, mangrove peat accumulated on top of the reef at a rate of up to 4.3 m per 1,000 years (Littler et al., 1995; Macintyre et al., 1995). On islands such as Twin Cays, Tobacco Range, and Carrie Bow Cay (see Fig. 1.1) there has been between 7.8 and ~16.0 m of peat deposition in ~8,000 years (Macintyre et al., 1995; Koltes et al., 1998), resulting in an average peat accumulation rate of 1 to 2 m per 1,000 years for much of the Holocene. Deposition was not steady but

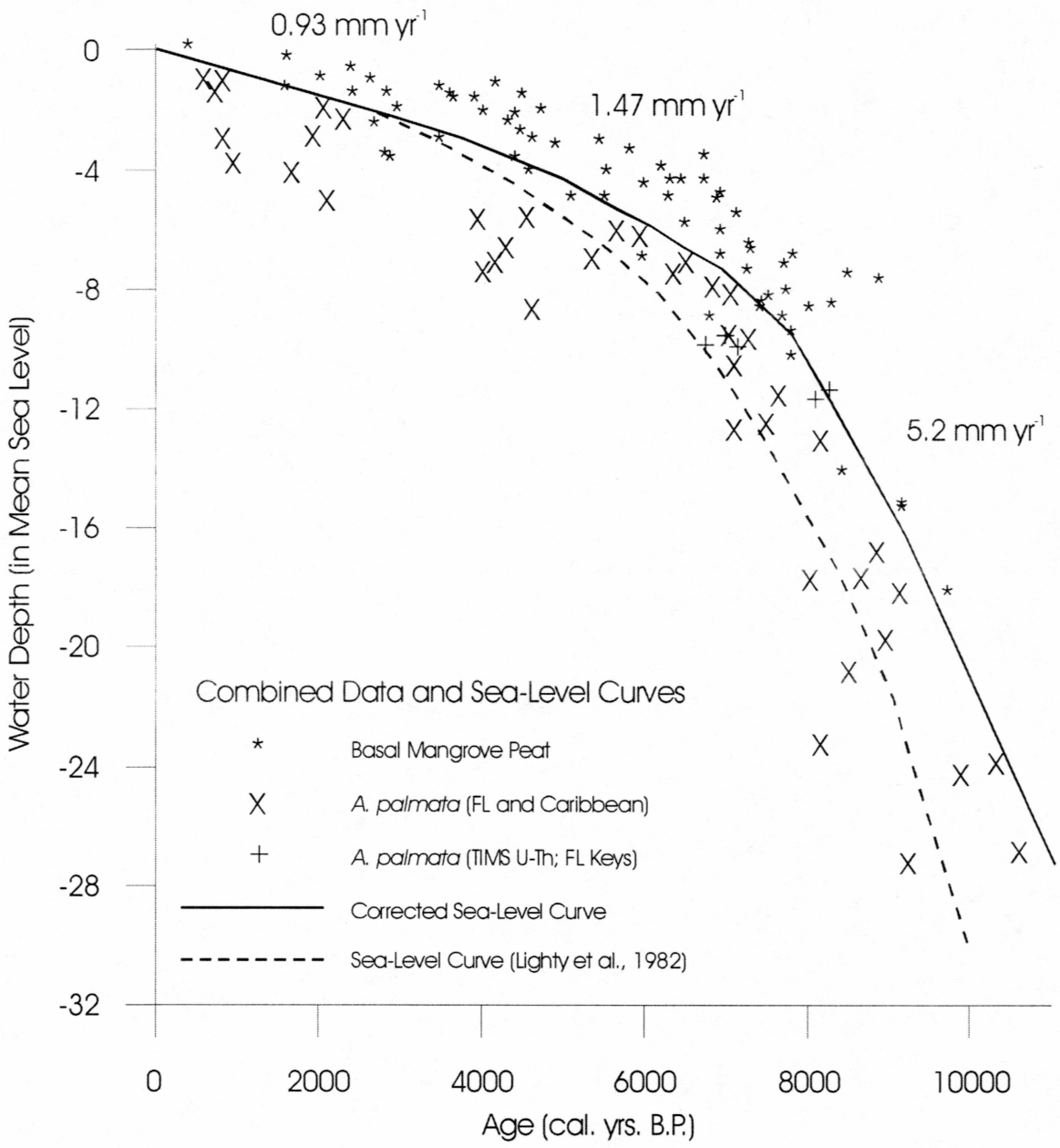

Figure 1.7
Adjusted sea level for the Caribbean Sea.
The dashed line is the previous sea level curve by Lighty et al. (1982). The solid line shows data presented by Toscano and Macintyre (2003). The corresponding rate of sea level change is given above the corrected sea level curve (modified from Toscano and Macintyre, 2003).

proceeded rapidly from ~8,000 through 3,000 cal. yrs. B.P. and then slowed (Littler et al., 1995; Macintyre et al., 1995; Wooller et al., 2003).

Approximately 3,000 cal. yrs. B.P., sea level rise slowed to less than 1 m per 1,000 years on Twin Cays and surrounding atolls (Littler et al., 1995; Macintyre et al., 1995). The rate of peat build-up also decreased to 1 m per 1,000 years (Littler et al., 1995). Peat accumulation rates have remained relatively stable since 3,000 cal. yrs. B.P.

Sea level changes recorded in the Belize coastal region are seen throughout the Western Atlantic (Littler et al., 1995; Toscano and Macintyre, 2003). Mangrove habitats in Central Amazonia suggest a similar rate and magnitude of sea level rise (Behling, 2002). In northern South America, sea level rise slowed around 7,500 ^{14}C yrs. B.P. At this time, mangroves first appeared in the coastal areas of the Brazilian Bragança peninsula in northeastern Pará state (Fig. 1.8) (Behling, 2002). Habitats in Central Amazonia may have been similar to those at Twin Cays, since mangroves began to colonize the Belize barrier reef islands around 8,200 cal. yrs. B.P. This suggests that early Holocene rates of Atlantic sea level rise were relatively consistent from Belize to northern South America.

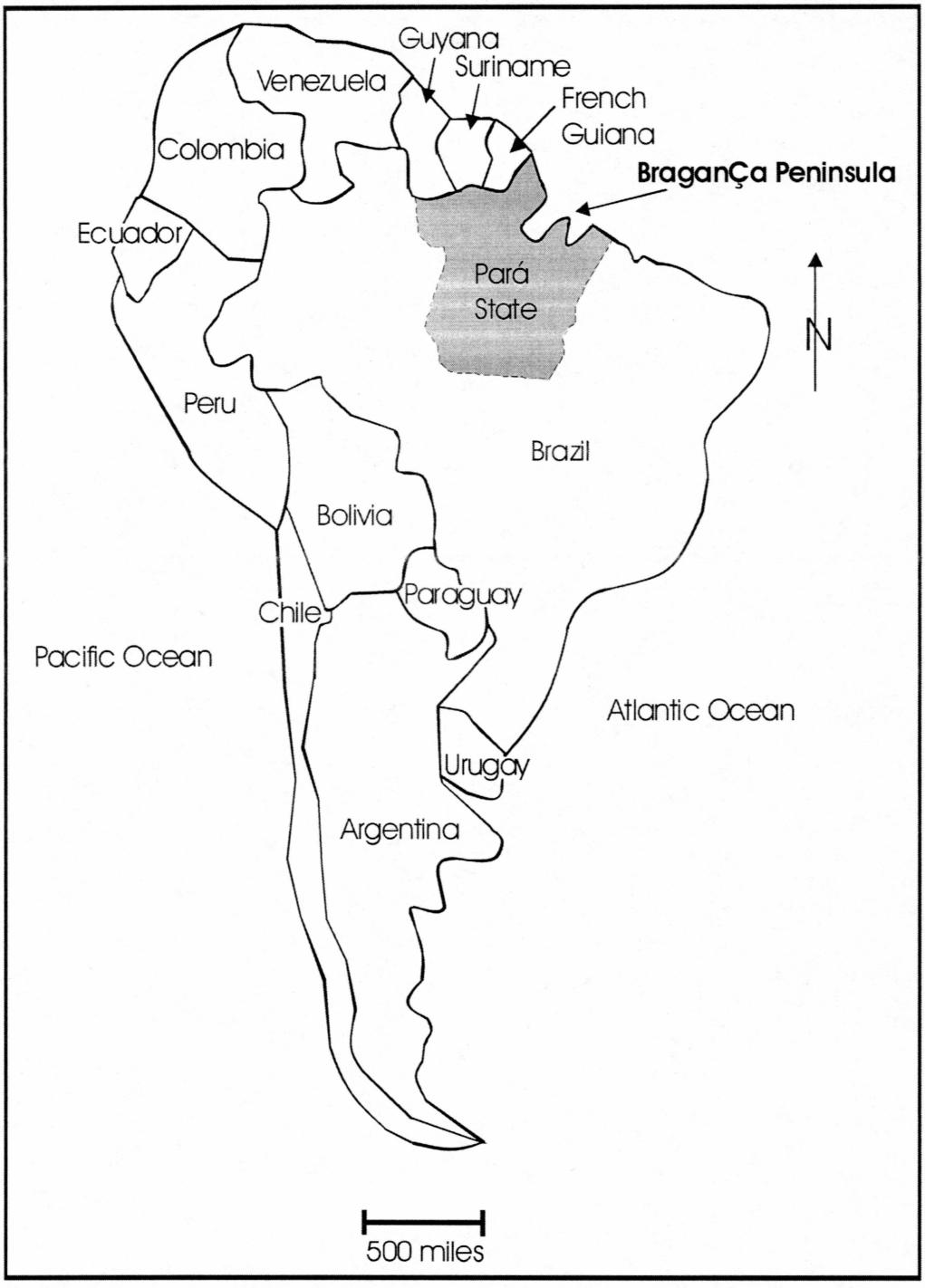

Figure 1.8
Map of South American showing the Bragança Peninsula in northeastern Pará state, Brazil.
(Modified from Behling et al., 2001).

1.3: Approaches

Three techniques are employed in an attempt to reconstruct the paleoenvironmental shifts that occurred on Twin Cays during the Holocene. Palynology is used to interpret vegetation shifts driven by ecological and climate changes. Stable carbon and nitrogen isotopes are used to understand *R. mangle*'s physiology, a proxy for nutrient availability and proximity to the coastline. Because stomatal density typically decreases with rising CO_2 levels, stomatal analysis is useful for reconstruction of atmospheric CO_2 composition (Royer, 2001; Kowenberg et al., 2003). These analytical techniques were applied to Twin Cays Core Two (TCC2) in order to reconstruct the history of Twin Cays and determine whether regional climatic changes observed in the Northern Hemisphere are also recorded on the Belizean islands.

1.3.1: Palynology

Palynology is a valuable tool for reconstructing past vegetation and climate change. By examining pollen deposited on the West Island of Twin Cays, it is possible to determine that mangroves began colonizing the islands ~8,200 cal. yrs. B.P. (Wooller et al., 2004). This method also allows for identification of three mangrove species; *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. Through microscopic analysis of the pollen grains, species can be distinguished based on

differences in size and sculpture. Thus, examining relative percentages of pollen throughout TCC2 is important for reconstructing changes in the vegetation surrounding the site.

Changes in vegetation inferred from shifts in pollen percentages can be driven by environmental factors such as hurricanes (Baldwin et al., 2001; Pascarella, 1998), sea level variation (McKee and Faulkner, 2000), nutrient shifts (Wooller et al., 2003), and long-term climate change (Leyden and Markgraf, 2002). *R. mangle* produce abundant pollen but *A. germinans* and *L. racemosa* are low pollen producers. In general, large amounts (>90%) of *R. mangle* pollen indicate that *R. mangle* trees were locally present (Behling et al., 2001; Wooller et al., 2004). Pollen concentrations of *A. germinans* between 10 and 30% suggest an *A. germinans* forest existed locally (Behling et al., 2001; Wooller et al., 2004). Pollen rain from mixed *R. mangle*/*A. germinans* stands contain less than 5% *A. germinans* pollen (Behling et al., 2001; Wooller et al., 2004). Mixed *R. mangle* and *L. racemosa* forests typically produce less than 5% *L. racemosa* pollen (Behling et al., 2001, Wooller et al., 2004).

Increases in *L. racemosa* and *A. germinans* pollen suggest a drier, inland location (Behling et al., 2001; Garcia and Holtermann, 1998; Koltes et al., 1998). Increased percentages of Myrsinaceae pollen can indicate recolonization following hurricane disturbance (Pascarella,

1998). *C. erectus* prefers sandy soils, and the presence of its pollen suggests a change in substrate (Woodroffe, 1995).

1.3.2: Stable Carbon and Nitrogen Isotopes

R. mangle leaves present throughout TCC2 can be used to determine shifts in phosphorus and nitrogen availability. As the nutrient availability in the soil changes, *R. mangle's* growth fluctuates between dwarf (<1.5 m) and tall (>1.5 m) (Feller, 1995; Woodroffe, 1995; Koltes et al., 1998; McKee et al., 2002). Dwarf *R. mangles* with $\delta^{15}N \leq -3‰$ indicate no phosphorus limitation; tall *R. mangles* are deficient in nitrogen and exhibit $\delta^{13}C \leq -27‰$ (Wooller et al., 2003). Analysis of stable carbon and nitrogen isotopes is the only method known to distinguish between the two growth types of *R. mangle*. Stable carbon and nitrogen isotope values derived from macrofossil leaf fragments of *R. mangle* indicate whether dwarf or tall *R. mangle* were present at the site of TCC2.

1.3.3: Stomata

Studies conducted on stomata have established an inverse relationship between stomatal density (number of stomata per unit area) and atmospheric CO_2 concentrations (Royer, 2001; Kowenberg et al., 2003). A recent Holocene study of Western Hemlock (*Tsuga*

heterophylla), conducted in Washington, Oregon, and British Columbia, shows that a decrease in stomatal density from 205 to 177 stomata/mm^2 corresponds to a CO_2 increase from 290 to 367 parts per million by volume (ppmV) (Kowenberg et al., 2003). This research concludes that a 1.99% decrease in stomatal density occurred with each CO_2 increase of 10 ppmV (Kowenberg et al., 2003).

Nearly all stomatal density data has been collected from temperate climates. Research on atmospheric CO_2 concentrations in tropical regions is surprisingly minimal (Hogan et al., 1991; Wooller and Agnew, 2001; Greenwood et al., 2003). It is often assumed that atmospheric CO_2 levels are consistent worldwide (i.e. Hogan et al., 1991; Royer, 2001; Greenwood et al., 2003), but this has not yet been demonstrated.

Mangrove stomatal densities have never been used to reconstruct historical carbon dioxide levels. A preliminary examination of the stomatal frequency (number of stomata per area) and size of mangrove stomata were measured on leaf fragments from various depths throughout TCC2 to determine whether *R. mangle* stomata are a reliable proxy for atmospheric CO_2 changes.

Chapter 2: Study Site- Twin Cays

2.1: Study Location

Twin Cays is composed of two islands, West and East, located ~12 km from the mainland of Belize at 16° 50' N, 88° 06' W (Feller et al., 2003; McKee et al., 2002; Wooller et al., 2004). These central American islands lie ~2.3 km leeward of the Belize barrier reef, roughly 5 km South of Tobacco Range atoll and 5 km Northeast of Carrie Bow Cay, in Central America (see Fig. 1.1) (Rützler and Macintyre, 1982; Woodroffe, 1995; Koltes et al., 1998). The two islands combined measure approximately 1.4 km long and 1.1 km wide (Woodroffe, 1995), with an area of 92 ha (Koltes et al., 1998). A small channel (0.5 to 2.0 m deep) separates the West and East islands (Woodroffe, 1995; Koltes et al., 1998). Two long cores, Twin Cays Core One (TCC1, 980 cm) and Twin Cays Core Two (TCC2, 780 cm) and five short cores have been collected from the islands using a Russian Peat Corer (Wooller et al., 2004). This study focuses on TCC2, a peat core taken from the West Island of Twin Cays.

2.2: Twin Cays Cores

TCC1 and TCC2 are composed of mangrove peat, as are cores recovered from other islands off the coast of Belize (Macintyre et al., 1995; Woodroffe, 1995; McKee and Faulkner, 2000). Atolls along the leeward side of the Belize barrier reef contain up to 10 m of continuous

peat overlying a limestone foundation (Woodroffe, 1995; Wooller et al., 2004).

In 2002, Matthew Wooller, Quinn Roberts, and Marilyn Fogel collected the Twin Cays cores with a Russian Peat Corer (see Wooller et al., 2004). TCC2 was gathered from an interior pond, which is covered by stands of dwarf *R. mangle* (Fig. 2.1) (Wooller et al., 2004). TCC1 was collected from a stand of taller *R. mangle* 0.25 km north of TCC2.

The majority of TCC2 (0-715 cm) is composed of mangrove peat containing *R. mangle* leaf fragments, roots, and other organic material. The basal 65 cm (715-780 cm) consists of fine-grained, silty, calcareous substrate lacking plant macrofossils. A color change from medium gray to reddish-brown accompanies the change from silt to peat.

TCC1 is primarily composed of mangrove peat with silty, fine-grained mud at the base. Basal dates for both cores are ~8,200 cal. yrs. B.P. The palynology of TCC1 was previously examined by Hermann Behling at the Centre for Tropical Marine Ecology and University of Bremen, Germany (Wooller et al., 2004). TCC1 is dominated by *R. mangle* pollen, with one notable exception. From 4,260 to 4,005 cal. yrs. B.P. (260-149 cm) the TCC1 site was dominated by Myrsine-type vegetation. Wooller et al. (2004) attribute this vegetation shift to a brief decline in sea level. One goal of this study is to determine whether this shift is recorded at the TCC2 site. If this vegetation shift at

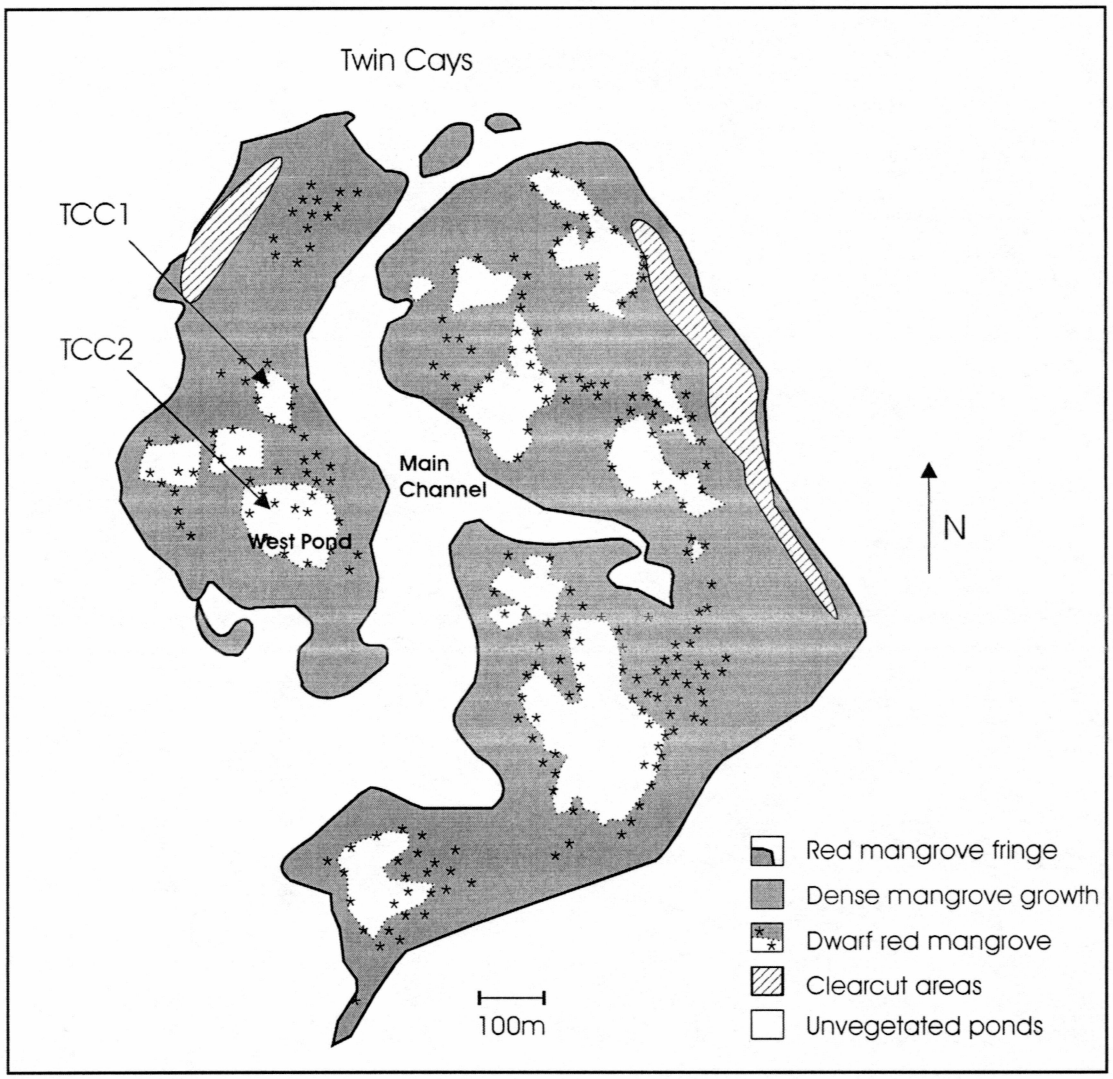

Figure 2.1
Current *R. mangle* zonation on Twin Cays.
Typically, tall *R. mangle* grow along the coast and along the channel separating the East and West islands. Dwarf *R. mangle* inhabit low regions surrounding the unvegetated ponds. Two clearcut areas are present, one on each island. The remainder of Twin Cays exhibits dense mangrove growth consisting of *R. mangle* with sparse stands of *A. germinans*, *L. racemosa*, and *C. erectus* (modified from Koltes et al., 1998).

~4,200 cal. yrs. B.P. is shown at TCC2 this may suggest a widespread change. A northern hemisphere dry event occurs at ~4,200 and may link these local changes to a global scale.

2.3: Vegetation

2.3.1: Introduction to Twin Cays Mangroves

The vegetation of Twin Cays consists primarily of mangroves with few herbs and grasses. Three types of mangroves are present: *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* [L.] Stearn. (black mangrove), and *Laguncularia racemosa* [L.] Gaertn. f. (white mangrove) (Koltes et al., 1998; McKee et al., 2002). *R. mangle* is the dominant species on the island today (Koltes et al., 1998; Feller et al., 2003; Wooller et al., 2004).

R. mangle height varies across Twin Cays in response to local environmental conditions. Dwarf *R. mangle* are generally found in interior lowland ponds and basins partially closed off from tidal input (see Fig. 2.1) (Woodroffe, 1995). Tall *R. mangle* (5-6 m tall) generally grow along the shoreline and line the banks of the main channel (Garcia and Holtermann, 1998; Koltes et al., 1998; McKee et al., 2002).

A. germinans grows inland of tall *R. mangle* in regions less frequently inundated with seawater (Garcia and Holtermann, 1998; Koltes et al., 1998). *A. germinans* trees are tolerant of high salt

concentrations and survive in areas with salinity ranging from 38-65 ppt (Kuenzler, 1974; Woodroffe, 1995; Garcia and Holtermann, 1998; McKee and Faulkner, 2000). At Twin Cays, *A. germinans* grows up to ~5 m tall and can be found with an under story of dwarf *R. mangle* or mixed with tall *R. mangle* (Woodroffe, 1995). *L. racemosa* trees are found only as scattered individuals on Twin Cays today (Woodroffe, 1995; Koltes et al., 1998). Typically, this species is found inland of the fringe *R. mangle*, in areas of higher elevation with less flooding and lower salinity (Garcia and Holtermann, 1998).

2.3.2: Other Species present on Twin Cays and Mainland Belize

Conocarpus erectus (buttonwood) is currently present on Twin Cays in small numbers (Woodroffe, 1995; Wooller personal observation, 2005). This species inhabits sandy substrates and is only found at the southern ends of the islands (Woodroffe, 1995). Herbs, grasses, and ferns are also present on Twin Cays (Woodroffe, 1995). Unvegetated flats, which are dry or shallow at low tide, characterize the island's interior and are often surrounded by dwarf *R. mangle* (Woodroffe, 1995; Koltes et al., 1998).

Pollen of a *Myrsine*-type plant is present in the TCC1 pollen record. This plant is not currently found on Twin Cays but can be found on the mainland of Belize (Table 2.1) (Wooller et al., 2004). Some types of Myrsinaceae (*Ardisia escallonioides* and *Myrsine coriacea*) are

Table 2.1
Myrsinaceae species present in Belize today.
This table lists the species of Myrsinaceae currently known to grow in Belize. The Myrsinaceae found in the Twin Cays pollen record has not been identified but is likely one (or more) of the species on this list (modified from Balick et al., 2001).

Species of Myrsinaceae in Belize
Ardisia compressa
Ardisia densiflora
Ardisia escallonioides
Ardisia nigrescens
Ardisia nigropunctata
Ardisia paschalis
Ardisia pellucida
Ardisia revolute
Ardisia schippi
Gentlea micrantha
Myrsine coriacea
Myrsine flordana
Parathesis cubana
Paranthesis donnell-smithii
Parathesis hondurensis
Parathesis membranacea
Parathesis oblanceolata
Parathesis rufa
Parathesis sessilifolia
Styogyne laevis
Styogyne turbacensis
Yunckeria amplifolia

documented disturbance indicators (Pascarella, 1998; Horn et al., 2001) that occur in areas undergoing sea level regression (Horrocks et al., 2002). After a hurricane, Myrsinaceae are often the first plants to recolonize a region (Pascarella, 1998). In Costa Rica, research has shown that Myrsinaceae quickly recolonize after forest fires; recovery of the original vegetation is seen in two years (Horn et al., 2001).

Chapter 3: Methods

3.1: Radiocarbon Dates

Rhizophora mangle leaf fragments were picked from TCC2 in order to obtain accelerator mass spectrometry (AMS) radiocarbon dates. Six samples (45, 295, 425, 620, and 712 cm) were prepared and dated. *R. mangle* leaf fragments were separated from the mangrove peat and washed with deionized water (DI). Each fragment was freeze-dried and stored in a glass vial. Leaf fragments were sparse at 45 cm depth, so 1 cm^3 of peat was dated instead. Samples were sent to Woods Hole Oceanographic Institution in Massachusetts for ^{14}C AMS dating. The Calib program 5.0.1 was used to convert the radiocarbon dates to calendar years before present (Stuiver et al., 1998; Stuiver et al., 2004).

3.2: Palynology

3.2.1: Laboratory Processing

Palynological processing of samples from TCC2 replicates Hermann Behling's methods for TCC1 (Wooller et al., 2004). Approximately 1 cm^3 (0.80-1.73 g) samples were collected at 10 cm intervals between 0 and 780 cm. A tablet of exotic *Lycopodium* spores was added to each sample in order to determine the pollen concentration (grains/cm^3) (Stockmarr, 1971). Pollen concentrations were calculated using the following formula:

$$\frac{(\text{fossil pollen counted})(\text{total number of markers})}{(\text{markers counted})(\text{volume})} = \text{pollen concentration}$$

Each sample was immersed in hydrochloric acid (HCl) for one hour to remove carbonates and then rinsed. All rinses were preformed by centrifuging the sample for three minutes, decanting the liquid, and then washing with deionized water (DI). This procedure was repeated three times. 10 ml of 10% potassium hydroxide (KOH) was added to the peat and the KOH/peat solution was heated for ten minutes in a 90°C water bath and then rinsed. The residue was then washed through a 250 μm sieve with DI to remove coarse organic matter. 10 ml of acetic acid was added to dry the sample prior to acetolysis. 10 ml of an acetolysis solution, a 9:1 ratio of acetic anhydride (CH_3COOH) and sulfuric acid (H_2SO_4), was added to each sample tube to break down cellulose. The tubes were put into a 90°C water bath for 18 minutes, stirring periodically, and then rinsed. After the acetolysis procedure, silty samples from the base of the core (710 to 780 cm) were treated with 52% hydrofluoric acid (HF) to remove silicate minerals. The samples were left in HF for 1.5 days, centrifuged, rinsed once with HCl and three times with DI. A 7-10 μm Nitex cloth sieve was used to remove clay-sized particles from the basal samples (710-780 cm). All samples were mounted in glycerin jelly.

3.2.2: Identification

Mangrove pollen species were identified based on comparison with type material of *R. mangle* and *A. germinans* and digital photographs of *L. racemosa*, *C. erectus*, and Myrsinaceae pollen (Fig. 3.1). The morphological descriptions listed in Thanikaimoni (1987), Moore et al. (1991), and Roubik and Moreno (1991) were also helpful in distinguishing the pollen grains.

Although all of the mangrove-type pollen grains found in the TCC2 samples are tricolporate, the four common species have distinguishing characteristics. *R. mangle* pollen averages 17 μm in the polar diameter and 22 μm in equatorial view, with psilate to scabrate sculpture. *A. germinans* produces larger pollen that averages 27 μm in diameter (polar view) to 38 μm (equatorial view) and has reticulate sculpture. *L. racemosa* pollen is psilate, approximately 25 μm in diameter and only visible in equatorial view. *C. erectus* has the smallest pollen (11-13 μm in equatorial view) with psilate exine and is only visible in equatorial view, occasionally with three pseudocolpi. Since there is no overlap in average pollen diameters, size was a major factor in identifying the mangrove pollen. Shape was also an important differentiating feature. *R. mangle*, *A. germinans*, and *C. erectus* pollen are relatively round, whereas *L. racemosa* appears distinctly oblong in equatorial view.

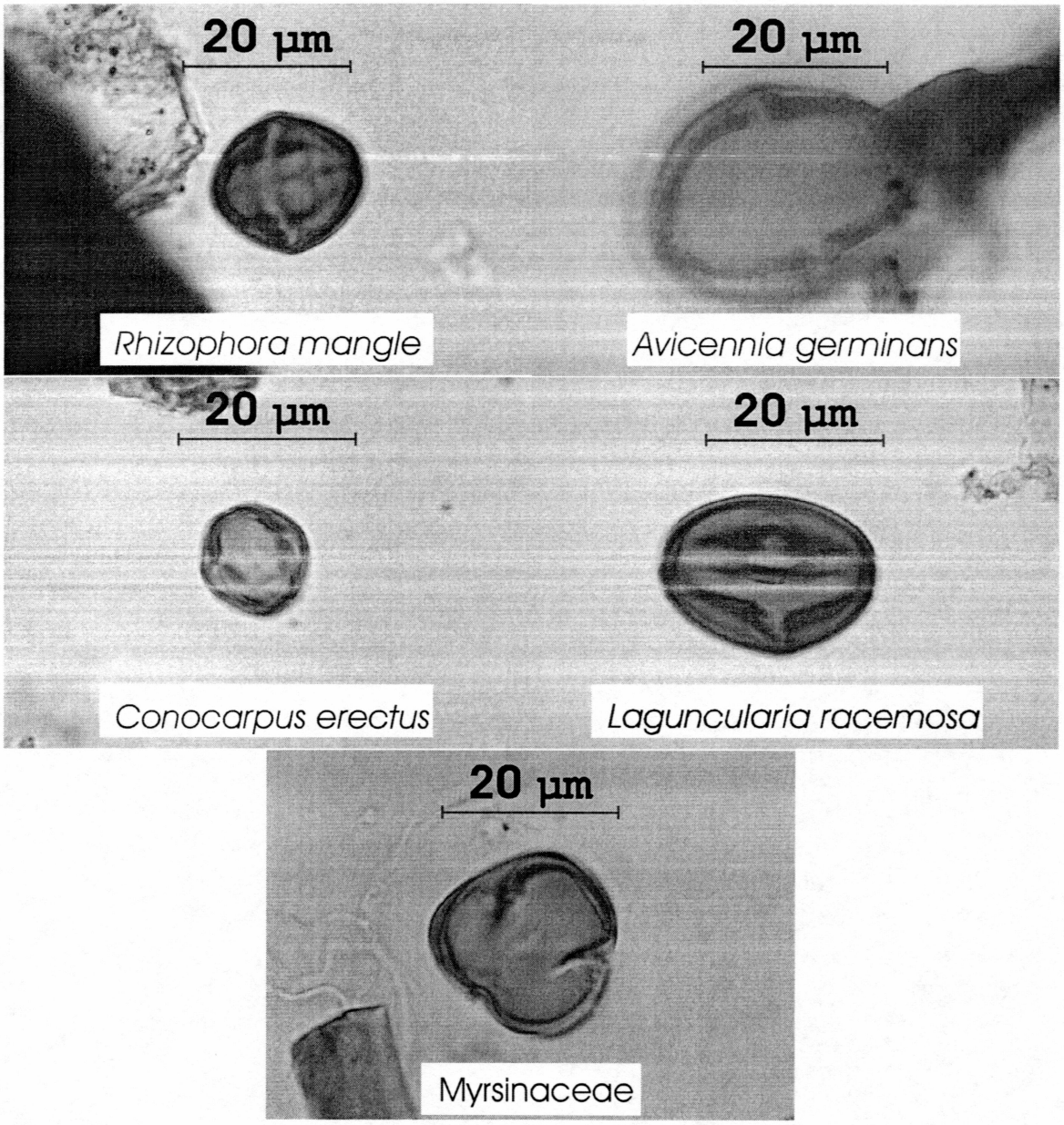

Figure 3.1
TCC2 pollen pictures.
Photographs of *Rhizophora mangle*, *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and Myrsinaceae pollen from TCC2.

R. mangle pollen was distinguished from *L. racemosa* primarily on the basis of size (noticeably smaller) and shape (round).

The other pollen types (including Myrsinaceae, *Pinus*, Poaceae, Asteraceae, and Palm) had significantly different morphologies, which made identification relatively simple. Myrsinaceae grains contain three to four colpi, average 25 μm (polar view) to 28 μm (equatorial view) in diameter, and are psilate. Myrsinaceae pollen is distinguished from mangrove pollen by the lack of pores. *Pinus* pollen is large (measuring 45-55 μm in distal view) and bisaccate. Asteraceae pollen is small (averaging 13-15 μm in polar view) and tricolpate, with echinate sculpture. Poaceae pollen grains are monoporate, spherical, moderately sized (generally 25-35 μm), and psilate. Grains of *Pinus* spp., Asteraceae, and Poaceae were identified using the key provided by Moore et al. (1991). A few large (~60 μm), psilate, trilete spores are present near the base of TCC2. These may be Sporopteridophyta or Polypodiaceae, as both are present on Twin Cays today.

3.2.3: Pollen Analysis

Due to low pollen concentrations, it was rarely possible to count and identify a minimum of 300 pollen grains and spores from each sample horizon (Table 3.1). Instead, a minimum of 100 grains were counted from samples with low concentrations. Less than 100 individual

Table 3.1
TCC2 pollen counts.
Actual number of pollen grains counted in TCC2 samples.

Low Concentration		Medium Concentration		High Concentration	
Depth	Grains	Depth	Grains	Depth	Grains
770	7	20	100	80	300
410	8	60	100	350	300
780	10	110	100	710	300
130	15	160	100	560	301
250	18	230	100	700	302.5
0	23	260	100	210	303
430	23	370	100	720	303
30	24	470	100	330	304
140	24	610	100	340	304
150	25	670	100	590	304
480	25	680	100	220	305
500	25	170	100.5	310	305
420	29	290	100.5	570	306
630	30	300	100.5	580	306
180	36	490	100.5	750	307
360	36	510	100.5	600	308
100	37	640	100.5	380	312
120	37	730	100.5	200	315.5
450	37	70	101.5		
620	37	320	102		
460	40	550	102		
50	41	660	104		
650	49	240	107		
740	49	280	109		
520	51	400	109		
90	60	10	110		
690	66	270	113		
		540	113		
		40	129		
		440	129		
		530	133		
		190	137		
		760	137		
		390	139		

pollen grains were counted and identified from extremely sparse samples. However, minor fluctuations in abundance create major changes in percent composition in sparse samples. For example, at 770 cm there are seven total grains (pollen and spores). Six are *R. mangle*, representing 86% of the total, and one is *Pinus* (14%). If one more *Pinus* were identified, the percentage would jump to 25% of the total. Therefore, only intervals with at least 100 identifiable pollen or spores are presented herein (77% of the total samples) in an attempt to minimize variance.

On the pollen diagram (Fig. 3.2) taxa are shown as a percent of the pollen sum, which includes all pollen grains and fern spores but excludes foraminifera test linings, diatoms, and fungal spores. Foraminifera test linings, diatoms, and fungal spores are reported in actual abundance per horizon.

3.3: Stable Carbon and Nitrogen Isotopes

Rhizophora mangle leaf fragments were collected at 5 cm intervals throughout most of TCC2 (0-605 cm). The sampling frequency was decreased below 580 cm, because leaf fragments are sparse at the base of the core (Fig. 3.3). From 605-730 cm, samples were taken at 10 cm intervals. Due to the complete lack of leaf fragments below 730 cm, bulk sediment samples were processed from 710, 720, 740, 750, and 760 cm.

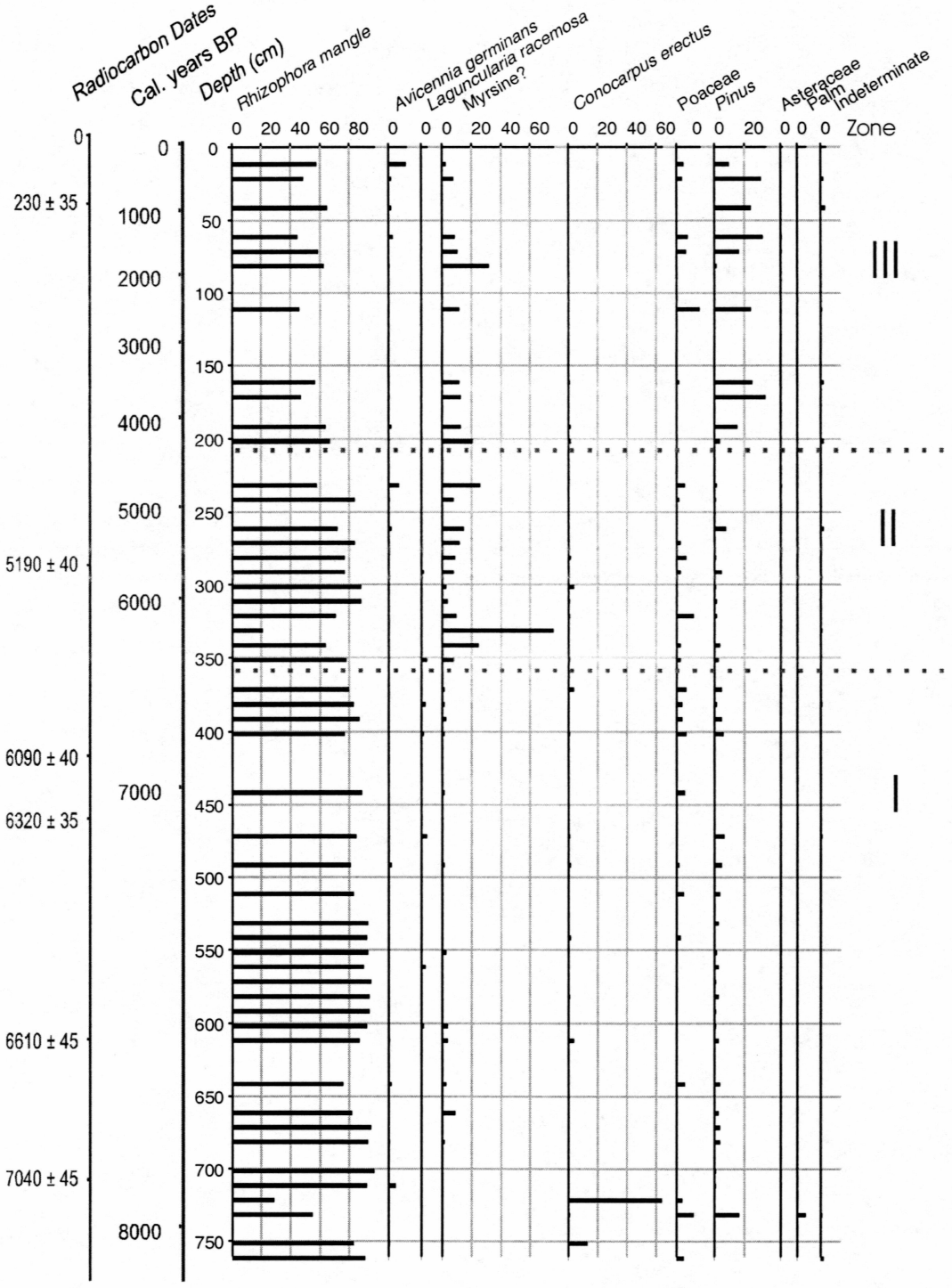

Figure 3.2
TCC2 pollen spectra and pollen zones (counted to at least 100 grains).

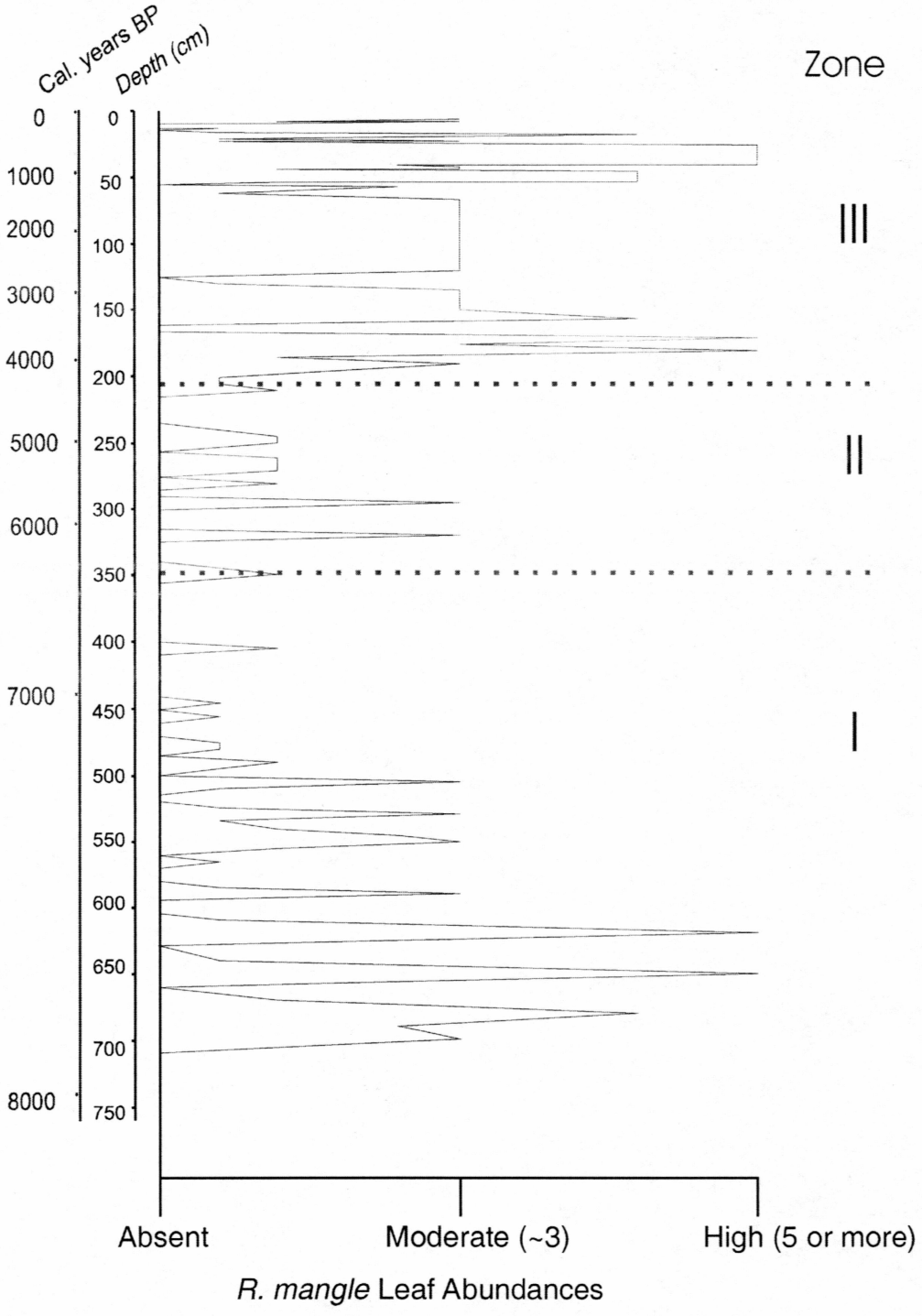

Figure 3.3
***R. mangle* leaf abundances**.
This graph shows the average abundance of *R. mangle* leaf fragments per depth in TCC2.

A bulk sample was not collected from 730 cm because a *R. mangle* leaf fragment was present at that depth.

R. mangle leaf fragments of various sizes (1-5 mm) were rinsed with DI and then freeze-dried. Once dry, 0.30-0.50 mg of powdered leaf was weighed into 3.75 mm tin cups sealed by crimping the cup with tweezers. *R. mangle* leaf samples were analyzed at the Carnegie Institute's Geophysical Laboratory in Washington D.C. An EA-IRMS (Finnigan MAT, DeltaplusXL) (Fig. 3.4) system was used to obtain the $\delta^{13}C$ and $\delta^{15}N$ values. Isotope ratios are reported relative to air ($\delta^{15}N$= 0.0‰) and Pee Dee Belemnite ($\delta^{13}C$= 0.0‰). Carbon and nitrogen values were calculated using the equation in figure 3.5.

Acedanalid (C_8H_9NO) was used to standardize the Elemental Analyzer- Isotope Ratio Mass Spectrometer (EA-IRMS) prior to processing bulk sediment samples and *R. mangle* leaf fragments. Acedanalid was analyzed periodically during sample processing to ensure consistency of the data. The standard was processed using 0.20-0.30 mg of material and 3.75 mm cups.

3.4: Stomata

Variations in the size and density of stomata typically reflect changes in atmospheric CO_2 concentrations (Ferris et al., 1996; Kouwenberg et al., 2003). Before linking stomatal fluctuations to shifts

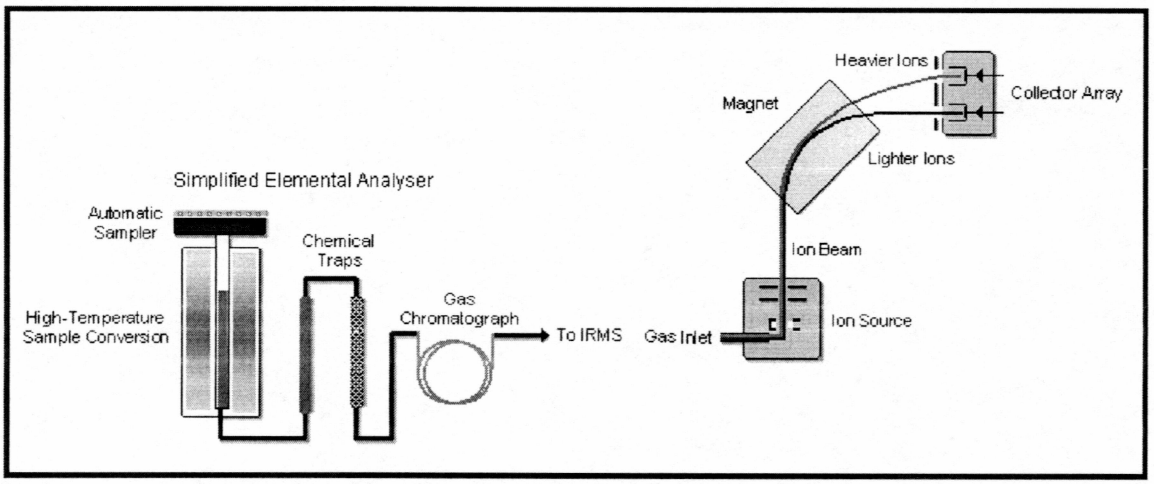

Figure 3.4
EA-IRMS system.
Elemental Analyzer-Isotope Ratio Mass Spectrometer system showing the method for recovering stable carbon and nitrogen isotope values.

$$\delta^{h}X = \left[\frac{\left(\frac{X^{h}}{X^{l}}\right)_{SAM}}{\left(\frac{X^{h}}{X^{l}}\right)_{STD}} - 1 \right] \times 1000$$

X is carbon or nitrogen
h is heavier isotope
l is lighter isotope
SAM is sample
STD is standard

Figure 3.5
Equation used to calculate stable carbon and nitrogen isotopes.

in atmospheric composition, it is necessary to establish whether mangrove stomatal densities vary over time and whether variations in stomata of a given species are correlated with changes in atmospheric CO_2 concentrations. Since such a study has never been conducted on *R. mangle*, this research determines stomatal size and density at 0, 12, 19, 26, 27, 28, 30, 33, 40, 43, 139, 149, and 525 cm depths and compares the data to the Holocene atmospheric CO_2 record.

R. mangle leaf fragments are present throughout much of the TCC2 core. Between 0 and 50 cm, samples for stomatal analysis were collected every centimeter. Between 50 and 605 cm, the sampling frequency was increased to 5 cm. The bottom portion of the core (605-730 cm) contains few leaf fragments, so the sampling interval was increased to 10 cm. The base of the core (730-780 cm) is composed of fine silt with no macrofossil leaf fragments (see Fig. 3.3).

Pictures of *R. mangle* leaf fragments were taken with a scanning electron microscope (SEM) at the University of Alaska Fairbanks. Fragments were viewed and photographed at 170x magnification. Two digital images of leaf surfaces were taken at each depth. Where possible, two separate leaf fragments were used. Three randomly selected 300 x 300 μm areas were examined on each photograph, and the stomata were counted by visual inspection. Stomatal counts were compiled for each area (six total per depth) and averaged. The total

number of stomata per image (~700 x ~900 μm area) was also tabulated in order to determine whether the number of stomata per 300 x 300 μm area is representative of actual stomatal density or whether a larger area must be evaluated. Stomatal length showed little variation per sample; so only four stomata were examined from each image or eight per horizon. A size estimate was obtained by averaging the lengths of stomata for each depth (Fig. 3.6).

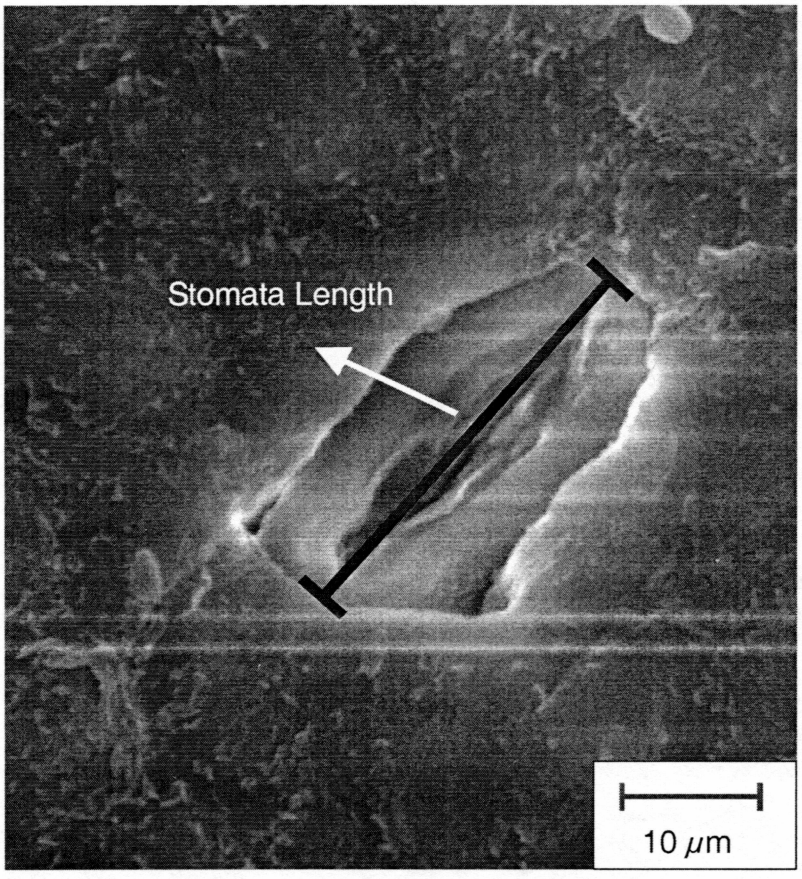

Figure 3.6
Measurements of stomata length.
The length of stomata were measured from images taken on a scanning electron microscope. This photograph is from 45 cm depth. The stomata is 28 μm in length.

Chapter 4: Results

4.1: Radiocarbon Dates

Six dates have been obtained from *R. mangle* leaf fragments from 45, 295, 425, 465, 620, and 712 cm depths in core TCC2 (Table 4.1). The calibrated ages correspond with AMS dates from the TCC1 core (Wooller et al., 2004), providing further evidence that the time of island formation is similar throughout the Belize barrier reef (Woodroffe, 1995).

4.2: Palynology

The zoning of a pollen diagram is useful in order to understand major changes in vegetation structure and dynamics. Three pollen zones are identified based on the relative percentages of mangrove species and total pollen concentrations in TCC2. Zones were distinguished based on visual inspection of the pollen diagrams.

R. mangle pollen dominates most of the assemblages (see Fig. 3.2). This is partially due to the fact that *R. mangle* produces greater amounts of pollen than *A. germinans* or *L. racemosa* (Behling et al., 2001). Thus, low percentages of *A. germinans* and *L. racemosa* may be a result of lower pollen production rather than sparse vegetation (Behling et al., 2001; Wooller et al., 2004).

Table 4.1
Radiocarbon and calibrated dates for TCC2.
Leaf fragments from six depth horizons have been processed for AMS radiocarbon dates. These are listed along with the calibrated dates. Ages were calibrated using Calib 5.0.1 (Stuiver et al., 1998; Stuiver et al., 2004).

Depth (cm)	C-14 Age	Calibrated (cal. years BP)	Age Error
45	240	230	± 35
295	5190	5950	± 40
425	6090	6900	± 40
465	6320	7240	± 35
620	6610	7500	± 45
712	7040	7860	± 45

4.2.1: Pollen Zone I

Zone I ranges from 780 to 360 cm depth (8,200 to 6,300 cal. yrs. B.P.). Assemblages from this interval are dominated by *R. mangle* pollen (56-98%) and exhibit low diversity. Myrsinaceae pollen is sparse throughout Zone I (0-20%), and *Pinus* pollen is also rare (0-17%). *C. erectus* appears in small concentrations (0-14%) except at 720 cm, where it comprises 64% of the assemblage. Other species present in Zone I include *A. germinans* (up to 5%), *L. racemosa* (up to 4%), and Poaceae (up to 13%). Sparse reworked pollen grains were found in the basal section below ~740 cm. These are substantially more wrinkled, cracked, and deteriorated than the other pollen grains. Poor preservation made identification of the reworked taxa difficult.

Fungal spores are relatively common at 730, 580, and 470 cm (61, 16, and 14 spores, respectively) (Fig 4.1). Foraminifera test linings are common at 730, 580, 490, 470, and 460 cm (30, 17, 11, 29, and 19 test linings, respectively). A spike in fungal spores and foraminifera at 730 cm precedes the dramatic increase in *C. erectus* at 720 cm. Basal depths (780-710 cm) were treated with hydrofluoric acid to remove silicates, thus it is not surprising that diatoms are absent from the lower portion of TCC2. However, diatoms remain rare throughout Zone I.

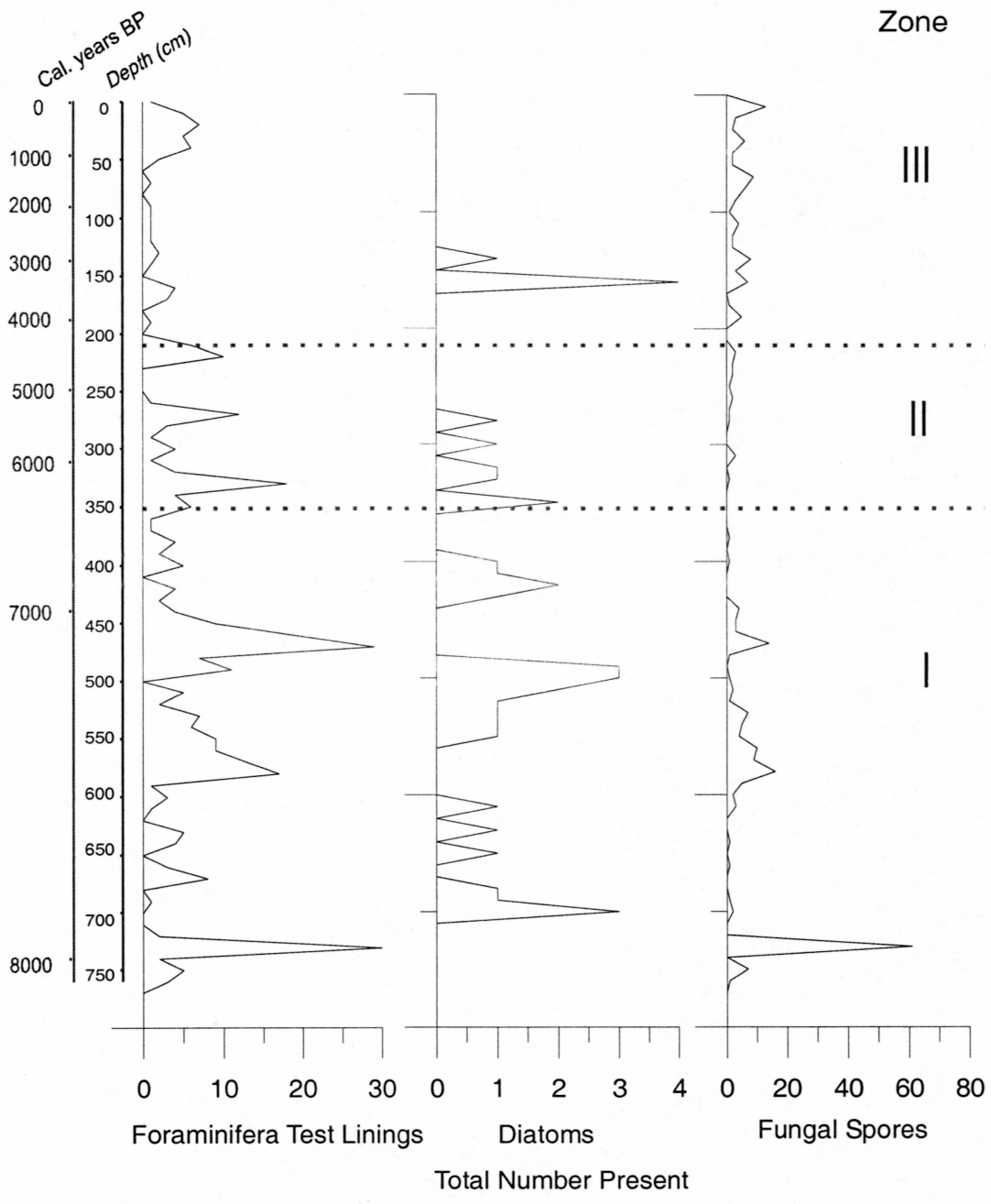

Figure 4.1
Non-pollen palynomorphs present in TCC2; fungal spores, diatoms, and foraminifera test linings.

4.2.2: Pollen Zone II

The boundaries of Zone II are placed at 360 and 210 cm (6,300 to 4,200 cal. yrs. B.P.). Moderate to dominant amounts (22-89%) of *R. mangle* pollen are present throughout, much like Zones I and III (see Fig. 3.2). Zone II is distinguished from Zone I by an increase in Myrsinaceae pollen (4-76%); moderate abundances of Myrsinaceae pollen and sparse *Pinus* pollen (0-8%) are characteristic of this zone. A major spike (76%) in Myrsinaceae pollen occurs at 330 cm (~6,300 cal. yrs. B.P.). Sparse to moderate amounts of *A. germinans* (up to 7%), *L. racemosa* (up to 5%), *C. erectus* (up to 5%), and Poaceae (up to 13%) occur throughout. Both fungal spores and diatoms are rare. The maximum number of foraminifera test linings (18) was recovered near the base of the zone at 330 cm depth.

4.2.3: Pollen Zone III

Assemblages between 210 and 0 cm depth (~4,200 cal. yrs. B.P. to present) are assigned to Zone III. This zone is distinguished from Zone II by high percentages of *R. mangle* pollen (41-75%) and moderate amounts of *Pinus* pollen (5-32%). Minor pollen taxa include Myrsinaceae (0-41%), *A. germinans* (0-12%), *L. racemosa* (0-2%), Poaceae (0-16%), and Asteraceae (0-2%). Diatoms are relatively abundant (four) at 160 cm, while numerous fungal spores (19) occur at 10 cm. Microforaminifera

test linings are sparse throughout Zone III; varying in abundance from zero to seven.

4.3: Stable Carbon and Nitrogen Isotopes

Basal (760-710 cm) bulk sediment $\delta^{13}C$ values reveal little variability between samples (-25.86 to -26.87‰) (Fig. 4.2). However, there is significant variability in the basal $\delta^{15}N$ values. Peat from 710 cm has a $\delta^{15}N$ value of +1.11‰, significantly lower than values from the underlying silt samples, which range from +6.15‰ (720 cm) to +7.62‰ (740 cm).

Stable isotope measurements obtained from *R. mangle* leaf fragments have a larger range than the basal bulk sediment values. $\delta^{13}C$ values obtained from *R. mangle* leaves range from a maximum of -22.16‰ (660 cm) to a minimum of -29.02‰ (110 cm). The highest $\delta^{15}N$ is +4.09‰ (65 cm) and the lowest value is -3.60‰ (90 cm).

Isotope values from Zone I are highly variable; $\delta^{13}C$ values range from -22.66 to -28.85‰ and $\delta^{15}N$ values from +3.74 to -3.13‰. The $\delta^{13}C$ values from Zone II show less variation, ranging from -24.76 to -27.69‰ while the $\delta^{15}N$ ranges from +3.50 to -3.49‰. $\delta^{13}C$ values for Zone III range between -23.13 and -29.02‰, while $\delta^{15}N$ values range from +4.09 to -3.60‰. Thus, Zone III offers a larger range of $\delta^{13}C$ and

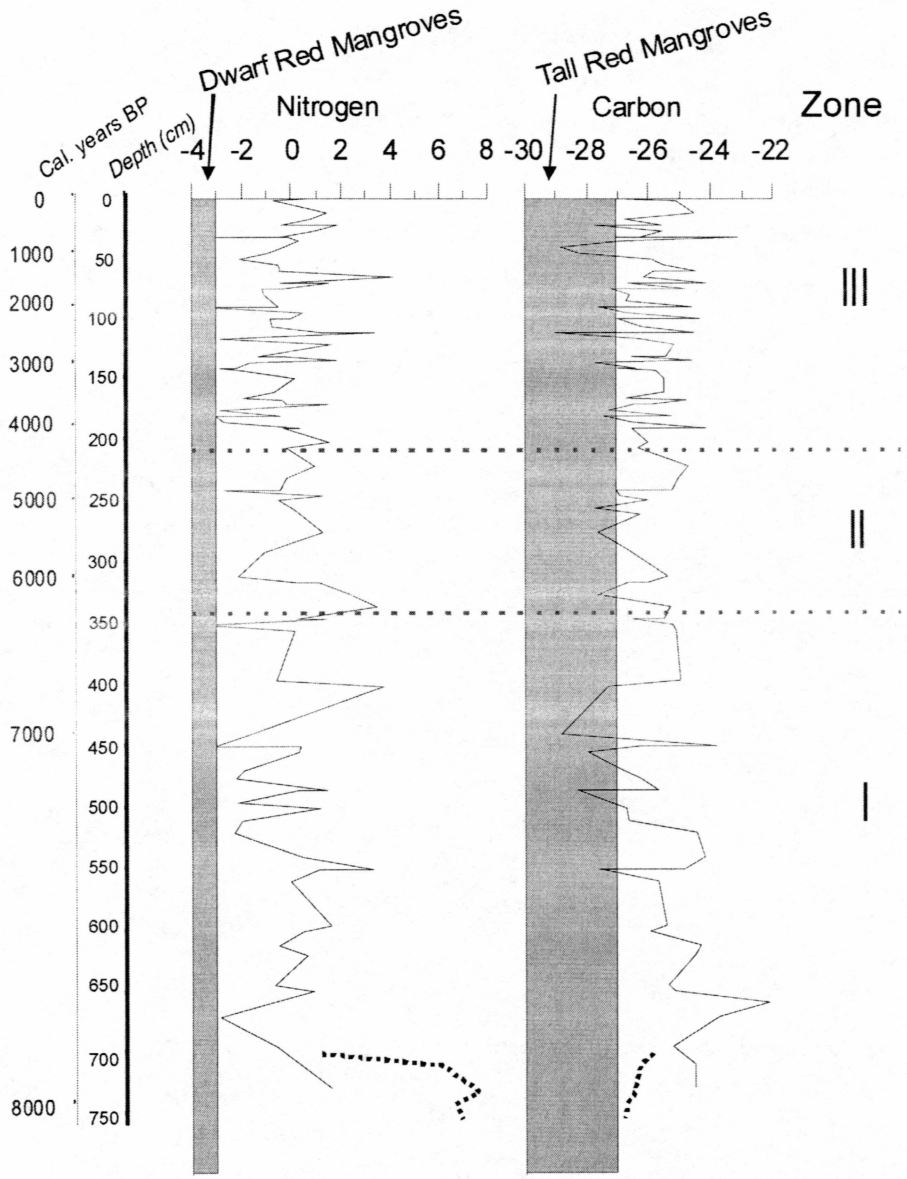

Figure 4.2
TCC2 stable carbon and nitrogen isotopes.
The solid line represents stable isotope values from *R. mangle* leaf fragments. The dotted line from 710 to 760 cm is data from bulk sediment measurements. Grey shaded areas represent the average range of stable isotope compositions form dwarf and tall *R. mangle* trees.

$\delta^{15}N$ values compared with Zone II, and basal samples exhibit high nitrogen values compared to the remainder of the core.

4.4: Stomata

Many of the *R. mangle* leaf fragments selected for SEM analysis were severely degraded. Of the 29 horizons studied, only 13 contained leaf fragments with visible stomata. The number of stomata per 300 μm^2 ranges from three to seven (Fig. 4.3). The minimum stomatal length is 34 μm and the maximum is 50 μm. A positive correlation exists between stomatal size and density; as size decreases, density also decreases. The average number of stomata per 700 x 900 μm area is approximately five and a half times the 300 x 300 μm sampling area. Since the 700 x 900 μm area is seven times larger than the 300 x 300 μm area the reduced size does not accurately reflect the stomatal density.

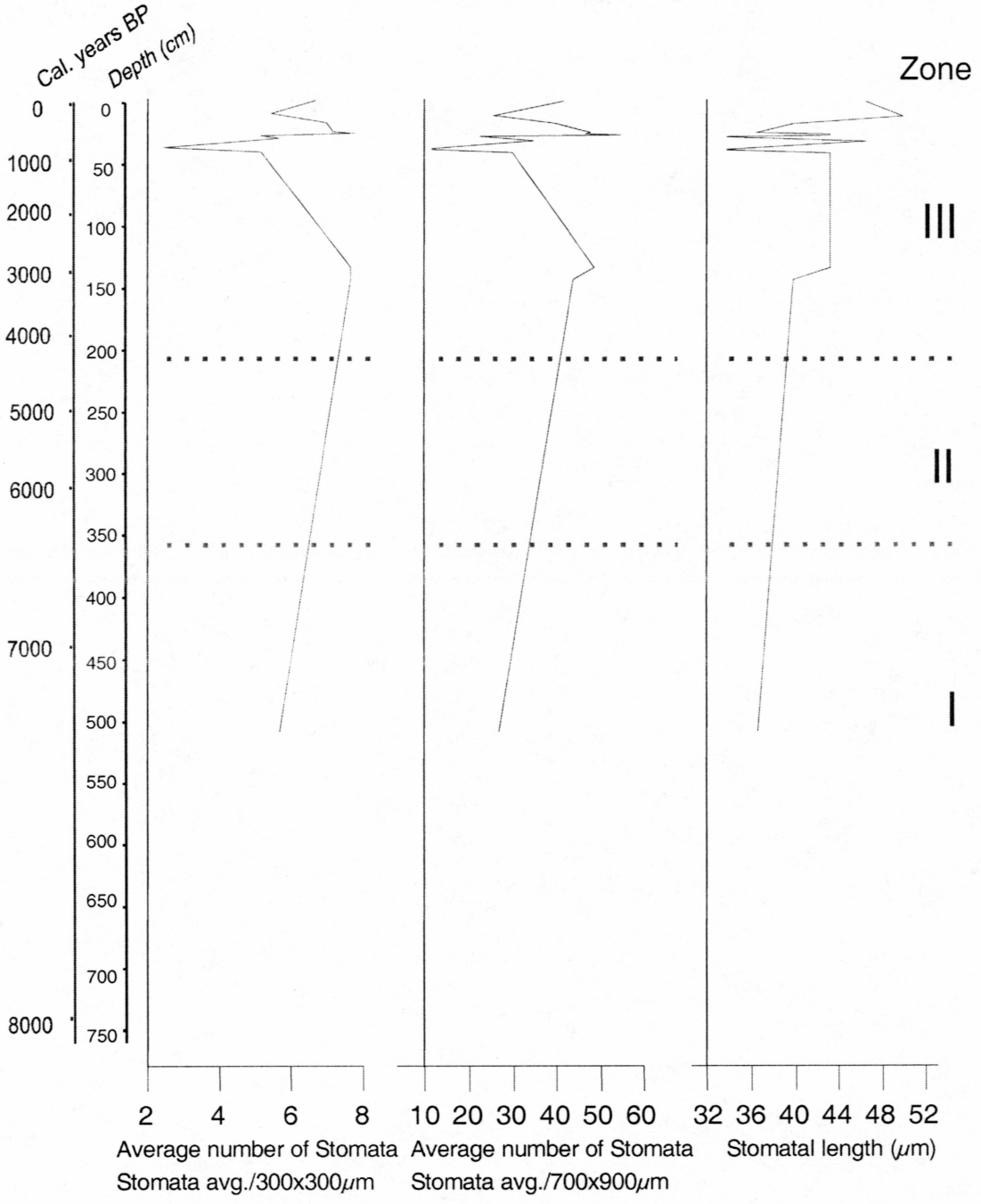

Figure 4.3
Averages of stomatal length and density.
Stomata were manually counted from digital SEM images. Average numbers are reported here. Stomatal lengths for each horizon are also averaged. The stomatal analysis focuses on the past 200 years, therefore the majority of data points are within the top 50 cm of TCC2.

Chapter 5: Discussion

Low elevation tropical islands are directly affected by a number of short and long-term environmental factors. Short-term events like hurricanes and tropical storms rapidly alter mangrove environments (Baldwin et al., 2001). In a matter of hours, strong winds destroy vegetation, while storm waves erode coastal areas. The storms do not last long, but the devastation is apparent for years (Baldwin et al., 2001). Gradual changes such as rising or falling sea level and climate fluctuations usually take place over centuries but can also occur on a decadal scale (Macintyre et al., 1995; Toscano and Macintyre, 2003). Typically, shifts that take place over a century or more are easier to recognize in the pollen record, because they are accompanied by a thicker depositional package; long-term shifts are often widespread and regionally apparent in the sedimentary record.

Significant palynological changes visible in a short section of core may indicate hurricane or tropical storm disturbance. Since the disturbance interval is brief, these events are challenging to identify and often overlooked. In contrast, long-term climate change can appear as a gradual shift in relative pollen concentrations that continues throughout the core. For example, in TCC2 pollen of *Pinus* is sparse throughout Zones I and II, but concentrations increase in Zone III, corresponding with a regional Holocene warming trend (Fig. 5.1). A climate change from

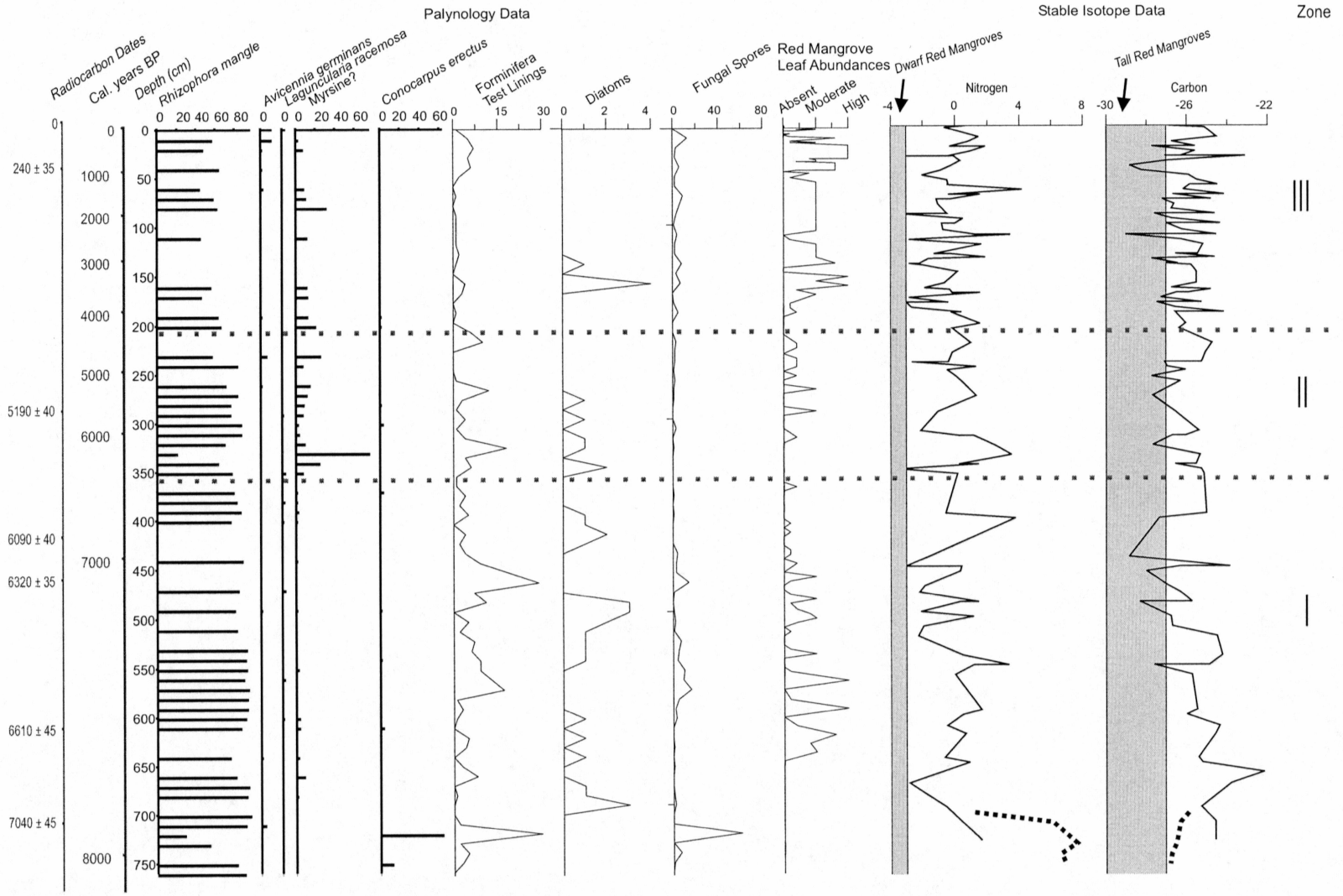

Figure 5.1
Summary figure comparing TCC2 data.

cool and dry with savanna-type vegetation to a warm and wet environment favoring forest taxa occurred throughout Central America during the mid-Holocene (~5,000 cal. yrs. B.P.) (Markgraf, 1993; Leyden, 2002). Although *Pinus* likely never grew on Twin Cays, its pollen is present in both TCC2 and TCC1. Heightened amounts of forest taxa (*Pinus*) on the mainland of Belize apparently resulted in an increase in relative *Pinus* pollen concentrations on Twin Cays.

5.1: Zone I (8,500 to 6,300 cal. yrs. B.P.)

Palynological data from the basal portion of TCC2 indicate that short-lived, decadal-scale changes occurred in the early Holocene during island formation. Around 7,950 cal. yrs. B.P. (730 cm), fungal spores dramatically increase (61 total), suggesting decomposition of organic material. Major storms can cause numerous trees to fall, littering the ground with leaves, branches, and other organic material (Baldwin et al., 2001). As plant material accumulates, decay and fungal spore production occurs (Kaushik and Hynes, 1971; Sridhar and Bärlocher, 2000).

Heightened percentages of *Pinus* and Poaceae are also characteristic of this interval, supporting the idea that a hurricane devastated *R. mangle* vegetation. Due to lower *R. mangle* pollen percentages, *Pinus* and Poaceae represent a larger portion of the pollen

sum. This may not mean that Pine and grass were present in the local vegetation. It only suggests that *R. mangle* pollen was less abundant, increasing the relative importance of windblown pollen from the mainland.

At 720 cm, *Conocarpus erectus* (buttonwood) is dominant and represents 64% of the pollen sum. By 710 cm, *R. mangle* returns to dominance, so the shift in local vegetation was temporary. It is possible that *R. mangle* vegetation was devastated by a hurricane, which led to low *R. mangle* pollen concentrations for an interval of less than 100 years, as determined by the sedimentation rate. The low *R. mangle* concentrations allowed *C. erectus* pollen to increase in percent. It is not likely that *C. erectus* actually increased in abundance. This plant prefers sandy soils and there is no visible change in the substrate at this horizon.

By 7,860 cal. yrs. B.P. (710 cm), *R. mangle* regains dominance in the pollen record. At this time an important composition change is visible in the core. Silty mud is replaced by mangrove peat, accompanied by a major change in $\delta^{15}N$ values. A drop in $\delta^{15}N$ from +7.66 to +1.11‰ suggests that the silt and peat have drastically different origins. On many Belize barrier reef islands, basal muds overlie the Pleistocene reef. Macintyre et al. (1995) explain that the mud is a reworked soil which formed on weathered Pleistocene limestone prior to flooding by rising sea

levels of the early Holocene. In the basal portion of TCC2, the majority of the pollen grains are highly degraded supporting the idea of a reworked soil. After 7,800 cal. yrs. B.P., mangrove pollen is predominant in TCC2, suggesting that the bulk of the pollen is locally derived from mangrove trees.

Elevated $\delta^{15}N$ values within the basal mud could be the result of bird droppings. Today, some islands in the Belize barrier reef are home to numerous shore birds. For example, Man o' War Cay is a low elevation island supporting colonies of blue footed boobies (Sula Neboxuii) and frigate birds (*Fregata maginificens*) which contribute large amounts of nitrogen-rich bird droppings to the sediment (Wooller et al., 2003a). A similar $\delta^{15}N$-rich environment likely prevailed on Twin Cays prior to the widespread establishment of mangroves. Subsequently, heightened amounts of mangrove peat deposition could have lowered concentrations of bird deposits after 7,852 cal yrs. B.P. (710 cm).

During the last glacial maximum sea levels were low, and many reefs became exposed above sea level. Twin Cays formed when rising Holocene seas swamped the elevated Pleistocene reef. As sea levels began to increase, swamping of these elevated land surfaces allowed for mangrove to colonization. Approximately 2,000 years after mangroves were established, a hurricane struck the island. This storm disrupted the vegetation, as evidenced by the dominancy of *C. erectus* over *R.*

mangle for ~90 years beginning at ~7,890 cal. yrs. B.P (720 cm). Immediately following this event, basal muds were replaced by mangrove peat (at 715 cm). This transition is recorded by a decline in $\delta^{15}N$ values and accompanied by a visual change in substrate. As mangrove vegetation flourished, the bird droppings became diluted with mangrove debris, resulting in lower nitrogen isotope values. In summary, between 8,500 and 6,300 cal. yrs. B.P. Twin Cays evolved from a barren silt island occupied by bird colonies to an island covered with a thriving mangrove forest.

5.2: Zone II (6,300 to 4,200 cal. yrs. B.P.)

Moderate amounts of Myrsinaceae pollen indicate that a mixed forest of Myrsinaceae and *R. mangle* surrounded the TCC2 site between 6,300 and 4,200 cal. yrs. B.P. According to Toscano and Macintyre (2003), the rate of Holocene sea level transgression decreased from 5.20 mm/yr to 1.47 mm/yr approximately 6,400 cal. yrs. B.P. If the accumulation rate of mangrove peat remained stable, a decrease in the rate of sea level rise would have created a drier site. Myrsinaceae is not typically found in saline environments (Balick et al., 2001); therefore I infer that parts of both the West and East islands were more elevated than today during Zone II.

At the nearby TCC1 site, 0.25 km north of TCC2, *Myrsine*-type pollen dominates from 4,275 to 3,990 cal. yrs. B.P. (260-149 cm) (Wooller et al., 2004). The pollen concentrations imply that Myrsinaceae grew at the site of TCC1. Some TCC1 pollen may have been carried to TCC2 via wind currents, but Myrsinaceae pollen concentrations up to 76% indicate that Myrsinaceae vegetation was growing onsite intermixed with the *R. mangle* forest.

Although Zone II records an increase in Myrsinaceae vegetation, *R. mangle* dominates most of the assemblages, representing 22 to 89% of the pollen sum. However, a decrease in the abundance of *R. mangle* leaf fragments combined with lower pollen concentrations indicates that the frequency of *R. mangle* in the local vegetation diminished during Zone II. Reduced competition from *R. mangle* may have created an environment favoring Myrsinaceae vegetation, or reduction of *R. mangle* pollen may have resulted in heightened Myrsinaceae pollen concentrations with no actual change in its frequency in vegetation.

The $\delta^{13}C$ and $\delta^{15}N$ from TCC2 mangrove leaves indicate a mixed stand structure (dwarf, tall, and transition *R. mangle*) for the majority of Zone II. Stable carbon isotopic values of ≤-27‰ are less frequent in Zone II than Zone I, appearing at 240, 255, 275, and 325 cm. This suggests that Zone II was initially dominated by dwarf *R. mangle*, but around 6,200 cal. yrs. B.P. mixed forests of tall *R. mangle* and

Myrsinaceae prevailed. Based on $\delta^{15}N$ values, purely dwarf *R. mangle* stands were only present at ~6,400 cal. yrs. B.P. The isotope data indicates that both nitrogen and carbon were readily available in Zone II soils ($\delta^{13}C \geq -27‰$ and $\delta^{15}N \geq -3‰$), leading to mixed stands or transition (both tall and dwarf) *R. mangle* throughout Zone II.

In summary, between 6,300 and 4,200 cal. yrs. B.P., Twin Cays was affected by sea level and vegetation changes. An increase in Myrsinaceae pollen concentrations at ~6,300 cal. yrs. B.P. (350 cm) is accompanied by a decrease in *R. mangle*. This could be interpreted as a result of a decrease in the rate of Holocene sea level transgression. The Twin Cays mangroves did not favor the drier environment, and Myrsinaceae became more abundant in the pollen rain.

5.3: Zone III (4,200 cal. yrs. B.P. to present)

Myrsinaceae pollen is less abundant in Zone III than Zone II. Throughout Zone III, *R. mangle* pollen concentrations increase as Myrsinaceae gradually disappears. This *Myrsine* decline is attributed to an increase in salinity. Today, *Myrsine* is not found on the islands of Twin Cays.

According to Toscano and Macintyre (2003), sea level transgression slowed from 1.47 mm/yr to 0.93 mm/yr at ~4,000 cal. yrs. B.P. A minor increase in *A. germinans* at ~4,035 cal. yrs. B.P. (190 cm depth) suggests

that the environment was slightly elevated compared to present, yet more saline than in Zone II. In conjunction with fluctuating isotope values, this salinity increase indicates that the core site lay inland, similar to its present location. Interior ponds can be stagnant, and evaporation increases salinity concentrations (Woodroffe, 1995; Garcia and Holtermann, 1998). As seawater inundation became less frequent, fewer microforminifera were washed over the site; foraminifera test linings are rare to absent in Zone III (see Fig. 4.1).

Although Zone III is dominated by *R. mangle* pollen, an abundance of *Pinus* distinguishes Zone III from Zones I and II. Compared to Zones I and II, the forest taxon *Pinus* is relatively common throughout Zone III. This is likely the result of an overall increase in forest taxa on the mainland of Belize. Beginning in the mid-Holocene, a regional climate shift to warmer and wetter conditions resulted in a change from savanna to forest vegetation in Central America (Markgraf, 1993; Leyden, 2002). As production of *Pinus* pollen increased on the mainland, more reached coastal islands, resulting in the elevated concentrations of forest taxa found in Zone III.

Locally, Zone III is composed of mixed dwarf and tall *R. mangle*. The $\delta^{13}C$ data indicate that tall trees repeatedly dominated the landscape (20, 40, 45, 75, 90, 100, 110, 135, 175, and 180 cm). From 4,200 cal. yrs. B.P. to present, TCC2 isotope values are highly variable, similar to

those from TCC1 (Fig. 5.2) (Wooller et al., 2004). The data suggest that shifts in the relative abundance of dwarf and tall *R. mangle* are caused by changes in nutrient availability and occur over brief intervals (see Fig. 4.2). Such shifts could be driven by tidal variation. Shifts in nutrient availability in seawater directly affect nutrient availability on the island

The isotope data suggest that the relative abundances of dwarf and tall *R. mangle* have fluctuated throughout Twin Cays history. Stomatal length and density are also variable (see Fig. 4.4). Nutrient fluctuations that favor dwarf or tall R. mangle also affect stomatal development, leading to length and density variations such as those seen throughout Zone III.

From 4,200 cal. yrs. B.P. to present, core site TCC2 was not located proximal to the shoreline. Zone III contains dwarf *R. Mangle* and scattered *A. germinans*, so the environment was probably more saline than in Zones I and II. Relatively low abundances of microforminifera and moderate amounts of *A. germinans* suggest that the core location lay further inland during Zone III. Today, the TCC2 site is located in the center of the West Island, surrounded by standing water, and dominated by dwarf *R. mangle*. This suggests that Twin Cays were increasing in size during Zone II.

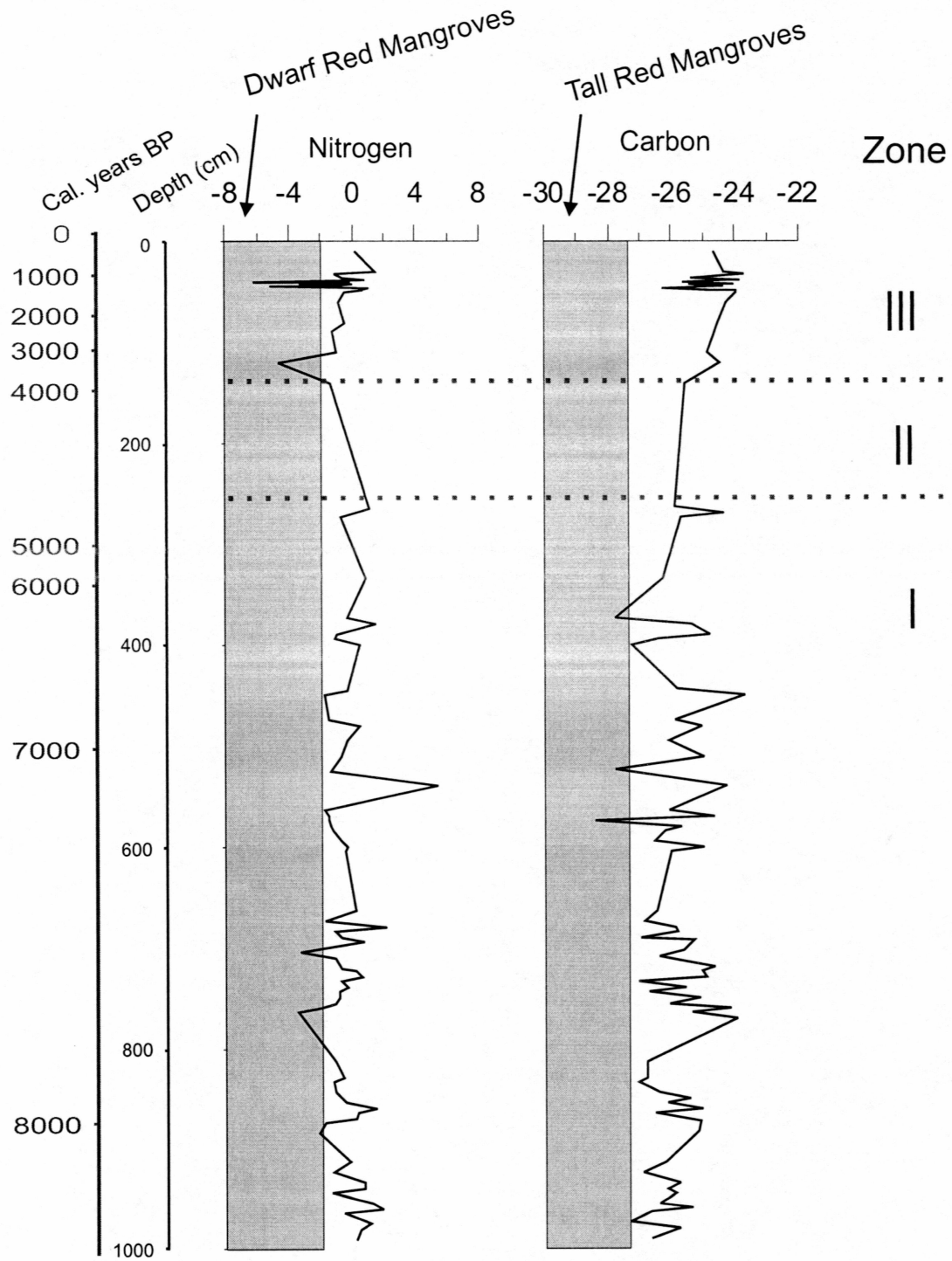

Figure 5.2
TCC1 stable carbon and nitrogen isotopes.
TCC1 isotope data by Wooller et al. (2004) is presented herein for comparison to TCC2 data. Grey shaded areas represent the average range of stable isotope compositions for tall and dwarf *R. mangle* trees.

5.4: Summary

As sea level rose during the early Holocene, Twin Cays developed on top of a coral reef. Island formation is accompanied by a gradual change in vegetation. *R. mangle* is the dominant vegetation type throughout TCC2, but at ~6,400 cal. yrs. B.P. Myrsinaceae pollen concentrations dramatically increase, perhaps as a result of a decrease in the rate of sea level rise. A mixed Myrsinaceae and *R. mangle* forest existed until ~4,200 cal. yrs. B.P., when Myrsinaceae gradually began to disappear, possibly due to increasing salinity. An environment favoring dwarf *R. mangle* and *A. germinans* over Myrsinaceae is apparent from ~4,000 cal. yrs. B.P. to present. A concurrent regional climate shift is also inferred from the palynological record. A marked increase in *Pinus* suggests that the regional climate became warmer and wetter after ~4,200 cal. yrs. B.P. Today, the TCC2 site is located inland and dominated by dwarf *R. mangle* with scattered *A. germinans.*

Major palynological and isotopic changes recorded in TCC2 correlate with global climate changes. Twin Cays may have formed during a global cool and dry event ~8,200 cal. yrs. B.P. (Markgraf, 1993; Alley 1997; Stager and Mayewski, 1997; Dean et al, 2002; Shuman et al., 2002, Kurek et al., 2004; Wooller et al., 2004; Lachniet et al., in press). During this time, sea levels were low (Toscano and Macintyre, 2003). At ~4,200 cal. yrs. B.P. a widespread dry period appears in the TCC2 record

as an increase in Myrsinaceae. This appears to correlate a widespread mid-Holocene dry period known from sites in the northern and southern hemispheres. Following this event, many northern hemispheric climates shifted toward warmer and wetter conditions, including the islands of Twin Cays.

Chapter 6: Conclusions

Regional variations in Holocene climate and sea level are evident across Central America. On Twin Cays, hurricanes and changes in nutrient availability directly affected the islands' vegetation. A multi-proxy approach combining palynology, stable carbon and nitrogen isotopes, and stomatal analyses is used to reconstruct local and regional paleoecological variations. The resulting reconstruction reveals interesting changes at ~8,000 and ~4,200 cal. yrs. B.P, times of global dry events.

Twin Cays began as a silt island ~8,200 cal. yrs. B.P. The onset of island formation corresponds with a widespread arid event at ~8,200 cal. yrs. B.P. This dry interval is apparent throughout the northern hemisphere (Gasse and Van Campo, 1994; Van Campo et al., 1996; Alley et al., 1997; Fowell et al., 2003; Adams et al., in press) and has been documented in the southern hemisphere (Stager and Mayewski, 1997). This event coincides with the formation of Twin Cays and has not been traced to the Central American region.

As northern hemisphere sea levels rose in the early Holocene, mangrove forests colonized the Belize barrier reef islands, and thick peat deposits accumulated (Woodroffe, 1995). On Twin Cays, mangroves began to deposit peat approximately 7,860 cal. yrs. B.P. The onset of mangrove peat deposition is recorded by changes in soil composition and

$\delta^{15}N$ isotope values. These shifts mark the widespread establishment of *R. mangle* vegetation on Twin Cays and, perhaps, a decrease in the marine bird population.

Beginning ~6,400 cal. yrs. B.P., the western Atlantic sea level transgression slowed from 5.2 mm/yr^{-1} to 1.5mm/yr^{-1} (Toscano and Macintyre, 2003), creating a drier environment on Twin Cays. It is likely that the island increased in size and elevation during this time. Higher elevation allowed Myrsinaceae to infiltrate the *R. mangle* forest. Between 6,400 and 4,200 cal. yrs. B.P., Myrsinaceae increases in the pollen record. This vegetation shift is interpreted as the result of increased elevation, which reduced the amount of *R. mangle* and heightened Myrsine concentrations.

Globally, arid events are recorded in Asia (Gasse and Van Campo, 1994) and North Africa (Gasse and Van Campo, 1994) ~4,200 cal. yrs. B.P. These arid events coincide with a vegetation shift on Twin Cays. At this time vegetation began to gradually return to *R. mangle* dominated forests. Abundant *R. mangle* and an increase in forest taxa on Twin Cays (especially *Pinus*) ~4,200 cal. yrs. B.P are likely the result of warmer and wetter conditions throughout Central America (Markgraf, 1993; Leyden, 2002). Similar changes are recorded at the nearby TCC1 site (Wooller et al., 2004). *Pinus* is not present on Twin Cays; pine pollen

presumably traveled ~12 km from the mainland of Belize. Thus, the shift in *Pinus* percentages records a regional climate change.

After ~1,500 cal. yrs. B.P., *A. germinans* increases in the pollen record, suggesting that the environment became more saline. Lower rates of sea level rise and less tidal inundation may have increased salinity in the interior. As a result, Myrsinaceae concentrations declined and Myrsinaceae is absent from the island today.

This research supports previous reconstructions of the Holocene environment of Twin Cays. Variations in the palynological and stable isotope values from TCC2 are a combination of short- and long-term factors. The island's primary influences are hurricanes, Holocene sea level transgression, and climate shifts toward warmer and wetter conditions during the late Pleistocene and Holocene. Significant events at ~8,200 and ~4,200 cal. yrs. B.P. occur concurrently with global events. The affects of these two arid intervals on the Central American region are poorly understood but may correlated with major shifts at Twin Cays.

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